

Eleven New Species in the Grammitid Fern Genus *Melpomene* (Polypodiaceae)

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ABSTRACT.—Based on extensive studies of grammitid ferns (Polypodiaceae) in the field and as specimens in various herbaria, eleven new species in the genus *Melpomene* are recognized from the Neotropics: *Melpomene albicans*, *M. caput-gorgonis*, *M. flagellata*, *M. huancabambensis*, *M. jimenezii*, *M. michaelis*, *M. occidentalis*, *M. paradoxa*, *M. personata*, *M. sklenarii*, and *M. vulcanica*. All are restricted to the Andes except for *M. personata*, which also extends to Mesoamerica and the Caribbean. The morphology and distribution of all species are illustrated.

KEY WORDS.—Andes, Caribbean, grammitid ferns, *Melpomene*, Mesoamerica

The genus *Melpomene* belongs to the grammitid ferns, which form a monophyletic clade within the Polypodiaceae (Schneider *et al.*, 2004) and comprise about 750 species (Parris, 2005) with a pantropical – southern temperate distribution (Parris, 1990, 2003). *Melpomene* was established as a genus solely on morphological characters (Smith and Moran, 1992) but was later supported as a natural monophyletic group in molecular analyses (Ranker *et al.*, 2004; Lehnert *et al.*, in print) that also confirmed some exclusions from and additions to the genus (Smith, 1995; León and Smith, 2003). Because of its young taxonomical age, the genus has never been revised as a whole. Partial revisions are available for Mexico (Mickel and Smith, 2004), Mesomamerica (Moran and Riba, 1995), and Brazil (Labiak and Prado, 2005), but these areas belong to the periphery of the total range of the genus, where a restricted assemblage of species and morphological emphasis caused by genetic drift may lead to an easier distinction of species. The majority of specimens come from the Andean region, where the genus occurs at 200–5200 m and displays the greatest morphological diversity.

In order to revise the whole genus, a total of 2100 collections from following herbaria were examined: AAU, B, BM, BHCB, C, COL, COLO, CUZ, GOET, K, LOJA, LPB, P, QCA, QCNE, RB, S, SP, TUR, UC, US, USM. Among them are 251 specimens collected by the author in Ecuador, Peru, Bolivia, and Argentina, giving him further insight about putative correlations between ecological conditions and morphological plasticity. As suspected from previous studies on grammitid ferns (Labiak, 2000; Rojas, 2001; León and

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Smith, 2004), several taxa in *Melpomene* were indentified as yet undescribed species.

Most of the following species have been collected prior to this study but were not recognized as something new. Instead, their morphological differences were dismissed as intraspecific variability or aberrations. In this study it was observed that some widespread species have a great morphological plasticity, reflecting a high potential to answer a wide array of ecological factors. Good examples are *Melpomene moniliformis* (Lagasca ex. Sw.) A. R. Sm. & R. C. Moran and *M. flabelliformis* (Poir.) A. R. Sm. & R. C. Moran, whose distributions cover almost the whole range of the genus, the latter species being the sole representative of the genus in the Paleotropics. They inhabit many different types of habitats and consequently vary in size enormously, which often is correlated with a change of the proportions of the segments and in the number of cells across the scale bases. Opposed to this, specialized species have to respond to a smaller amplitude of biotic and abiotic factors and consequently should display a lower morphological variability. In respect to the absolute ranges of the morphological variability, this leads to an apparent incongruence among the species descriptions presented here. The reasons for the respective recognition of a species are given in the comments following the descriptions.

Terminology follows that of Lellinger (2002). Grammitid ferns are beset with two types of laminar indument that are distinct and not part of a homologous series. The term “seta” has often been applied to the stiff, darkened hairs that frequently occur in grammitid ferns and also in *Melpomene* (Smith and Moran, 1992; Labiak and Prado, 2005). The same treatments used the term “hairs” for the paler, often branched trichomes found mainly on young petioles and rachises in *Melpomene*. However, I find that the so-called “setae” are differently developed within *Melpomene*, sometimes representing species autapomorphies and sometimes reflecting different growth conditions. For example, the “setae” of *M. firma* (J. Sm.) A. R. Sm. & R. C. Moran are usually quite short and patent, for which the term “acicular hairs” would be more fitting (Lellinger, 2002). In *M. flabelliformis* and many related species, the “setae” are sometimes flaccid and twisted, often occurring with properly developed (i.e., straight and rigid) “setae”. Such flaccid trichomes are better described as “ciliform hairs” (Lellinger, 2002). For the rigid “setae,” the term “setiform hairs” is available (Lellinger, 2002). Furthermore, used in Latin diagnoses, the term “seta” would translate as “bristle” (Stearn, 2004), which is a notably different structure (Lellinger, 2002) that is not found in *Melpomene* or other grammitid genera. I will use the terms “ciliform,” “setiform,” and “acicular hairs” to describe the simple pluricellular trichomes that are usually dark red in color with acute tips, and “clavate hairs” for the minute, simple and branched, pluricellular hairs that are pale in color and bear clavate cells at their apices or along their length. This second type of hairs has been referred to as “glandular” (Parris, 2005) and they appear to be homologous to the secretive gland-bearing branched hairs of *Zygophlebia* (Bishop, 1989), but a secretive nature was not observed in the hairs of *Melpomene* so far. The same can be

stated for the “glands” that occur on the scale apices of all *Melpomene* species. They are thin walled cells that are arranged singly or as pluricellular papillae or branched clavate hairs at the tips and rarely also along the margins of the rhizomes scales, strongly resembling the clavate hairs of the fronds. They are here simply referred to as apical and marginal cells. Scales are only found on the rhizomes and sometimes on the petiolar bases.

The dimensions of the segments are measured with the midveins as cardinal points, which are assumed as medial lines in the central parts of the segments between the sori if they are obscure. Segment length is measured along the midvein from segment tip to rachis; segment width is taken as the orthogonal line at half of the length. The dimensions are more useful if the width is taken in the central part of the segments because deltate segments are usually strongly decurrent onto the rachises in their proximal half and width taken here may vary considerably.

Melpomene albicans Lehnert, *sp. nov.* TYPE.—BOLIVIA. **Santa Cruz:** Prov. Caballero, Comarapa, ca. 1 km de Siberia hacia Torecillos, 17°49'S, 64°40'W, 2650 m, 18 Mar 2003, *Lehnert 714* (holotype GOET; isotypes LPB, UC). **Figs. 1, 7A.**

A *Melpomene personata* laminis abaxialiter albicantibus, a *M. youngii* (Stolze) B. León & A. R. Sm. pilis pluribus in soris confertis praestans.

Plants predominantly epiphytic or epilithic, growing in moss layers. *Rhizomes* moderately to short-creeping, horizontal (Fig. 1A), 0.8–1.2 mm diam., sometimes with short branches (5–10 mm) held at right angles. *Fronds* to 23 cm long, erect (Fig. 1A) or patent, inserted onto the rhizome at acute angles, but often held at nearly right angles to the rhizome, closely arranged (internodes 2–5 mm) but not caespitose (Fig. 1A). *Scales* 3.0–5.0(–7.5) × (0.3–) 0.6–0.8(–1.0) mm, (12–)16–20(–22) cells wide, lanceolate, clathrate (Fig. 1B), dark brown to brown, strongly iridescent, bases cordate to broadly cordate, tips acute to short-attenuate; apical cells 3–8, in a nodding cluster or palmate arrangement (Fig. 1C). *Petioles* (24–)35–85 mm long, 0.5–0.8 mm thick, marginate from the laminar bases, most parts terete, glabrous to glabrescent with dark brown setiform hairs 0.75–1.2 mm long (Fig. 1D); simple and branched clavate hairs (0.1–0.3 mm) of crosiers and young fronds often persist in older fronds. *Laminae* firm-chartaceous, to 120–75 × 18–35 mm (2/3 to 4/5 of frond length), narrow-elliptic to elliptic (widest in the middle), rarely obovate (widest above the middle), cuneate or somewhat tapering at bases, acute to attenuate at tips (Fig. 1A); surfaces abaxially whitish to white, often yellow or ochre when dried, usually eliminated if treated with alcohol. *Rachises* dark brown to black, planar and slightly sunken between segments adaxially (Fig. 1F), hemispherically protruding abaxially (Fig. 1E), with few to many branched clavate hairs like on petioles, otherwise glabrous or with scattered acicular hairs. *Segments* to 9.0–16.0 × 1.2–2.6(–3.0) mm (6–8 times longer than broad), flat, weakly ascending (80–70°), equilateral at bases or weakly decurrent basiscopically, fully adnate, linear-oblong to long-deltate,

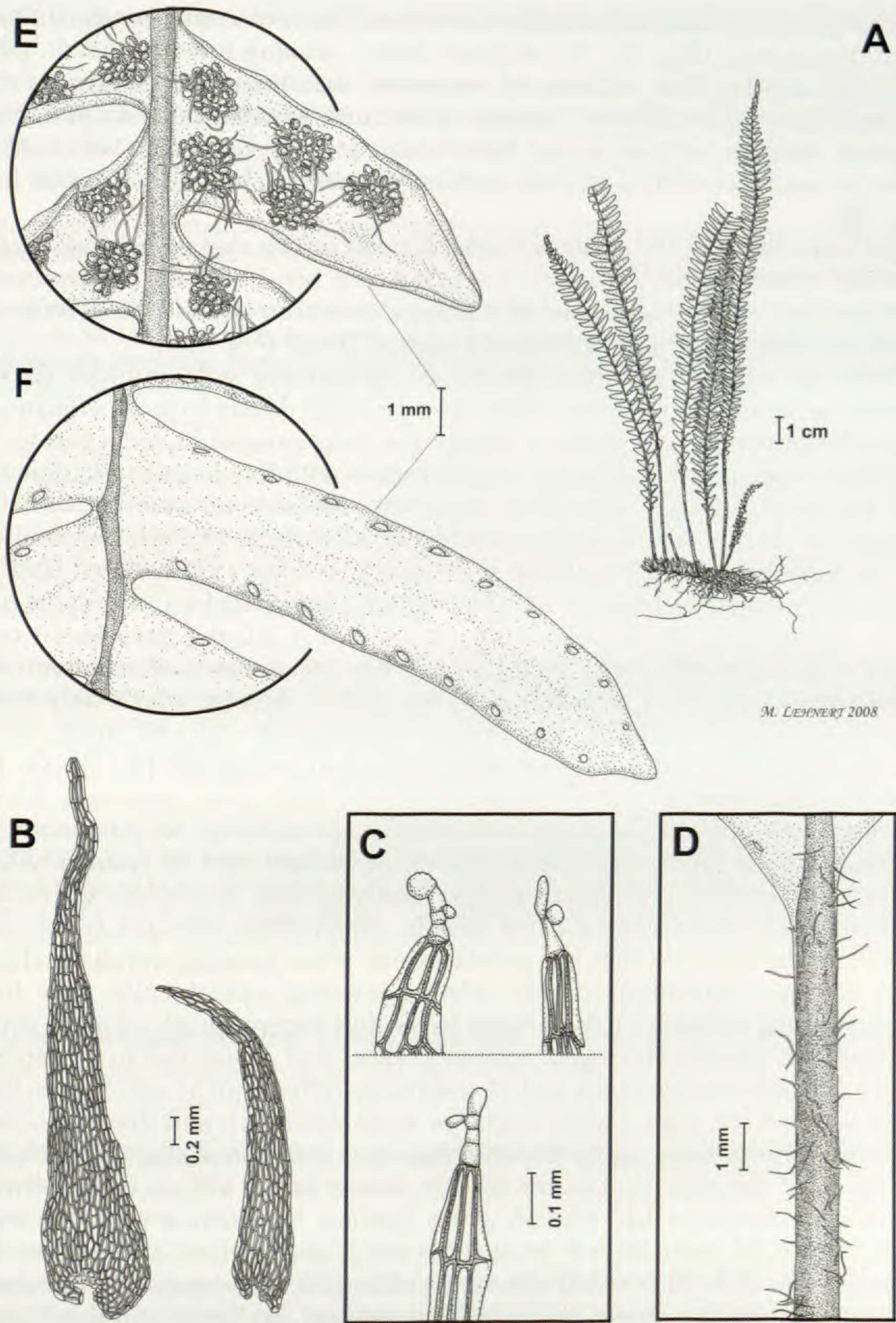


FIG. 1. *Melpomene albicans*: A. habit; B. scales, different sizes; C. detail of scale apices; D. petiole, upper part; E. fertile segment abaxially; F. segment adaxially (all from *Lehnert 717*, GOET).

the tips obtuse or short-acute; midveins not visible, or obscurely so abaxially in dried specimens (Fig. 1E, F), without hairs; proximal 1–7 segment pairs markedly smaller than subsequent segments, sometimes the lowermost 1–4 segment pairs auriculiform; stomata sometimes visible as rusty red dots; segment margins without hairs; hydathodes present (Fig. 1F). *Sori* 2–8(–9) pairs per segment, with 4–10 dark-castaneous setiform hairs 0.5–0.8 mm long (Fig. 1E).

The name refers to the white wax-like deposit on the abaxial laminae (Latin, *albicans* = being white).

Melpomene albicans grows in elfin forests, cloud forests, and moist montane forests at 1500–3400 m in Bolivia and eastern Brazil (Fig. 7A).

There are only a few other species of *Melpomene* with whitish abaxial laminar surfaces. Among these, *Melpomene youngii* differs from *M. albicans* in being almost completely glabrous (rarely 1–2 hairs present in some sori vs. 4–10 hairs in sori, petioles glabrous to glabrescent with few hairs in *M. albicans*) and the more strongly ascending segments; *Melpomene sodiroi* (Christ & Rosenst.) A. R. Sm. & R. C. Moran matches *M. albicans* in the hair distribution, but has gibbose segments with the sori slightly to deeply sunken (vs. laminae planar with superficial sori in *M. albicans*) and larger scales (on average $6.0\text{--}9.0 \times 1.0\text{--}1.2$ mm, 24–30 cells wide vs. $3.0\text{--}5.0 \times 0.6\text{--}0.8$ mm, 16–20 cells wide) with characteristically long tapering tips (vs. acute to short-attenuate). *Melpomene erecta* (C. V. Morton) A. R. Sm. & R. C. Moran, which only rarely has white laminar surfaces, has thicker rhizomes (to 2.4 mm diam. vs. to 1.6 mm diam. in *M. albicans*) and wider scales (on average 38–60 cells vs. 16–20 cells across base).

Melpomene albicans belongs to a complex comprising *M. personata*, *M. peruviana* (Desv.) A. R. Sm. & R. C. Moran, *M. sodiroi*, and *M. youngii*, which all have horizontally creeping rhizomes, relatively dark, lanceolate scales, and predominantly downward pointed fronds. *Melpomene albicans* is the only species in the complex that has patent fronds when growing epiphytically or even strongly ascending fronds when growing epilithically. All have relatively long setiform/ciliform hairs in the sori except for *M. youngii*, where the hairs are usually lacking or relatively short and sparse (up to 2 hairs per sorus). *Melpomene personata* and *M. peruviana* differ from *M. albicans* in their green laminae (vs. with a white wax-like layer abaxially), and they often have setiform/ciliform hairs along the midveins and sometimes single hairs along the segment margins, which are always absent in *M. albicans*. *Melpomene peruviana* sometimes has whitish green laminae but lacks a wax-like layer. Additionally, *M. peruviana* is on average much smaller than *M. albicans* and *M. personata* (2.5–10.0(–17.5) cm vs. to 17.5–25.0 cm), tends to form dense tufts or cushions (vs. single plants or loose groups), and grows predominantly epilithic in drier or cooler habitats than the other two species (mostly epiphytic in elfin forests and wet montane forests).

The specimens of *Melpomene albicans* from Brazil are less variable in size than the Bolivian specimens. They are smaller on average and have shorter petioles; Ribas et al. 3080 (UC) has also rather densely hairy petioles. The

Brazilian plants are more easily confused with *M. xiphopteroides* (Liebm.) A. R. Sm. & R. C. Moran than the Andean population because the white laminar layers are less developed and the scales are smaller, and thus closer to the morphological spectrum of *M. xiphopteroides*. However, even weakly hairy plants of *M. xiphopteroides* have more setiform/ciliform hairs on the rachises than *M. albicans*, in which the rachises are usually glabrous.

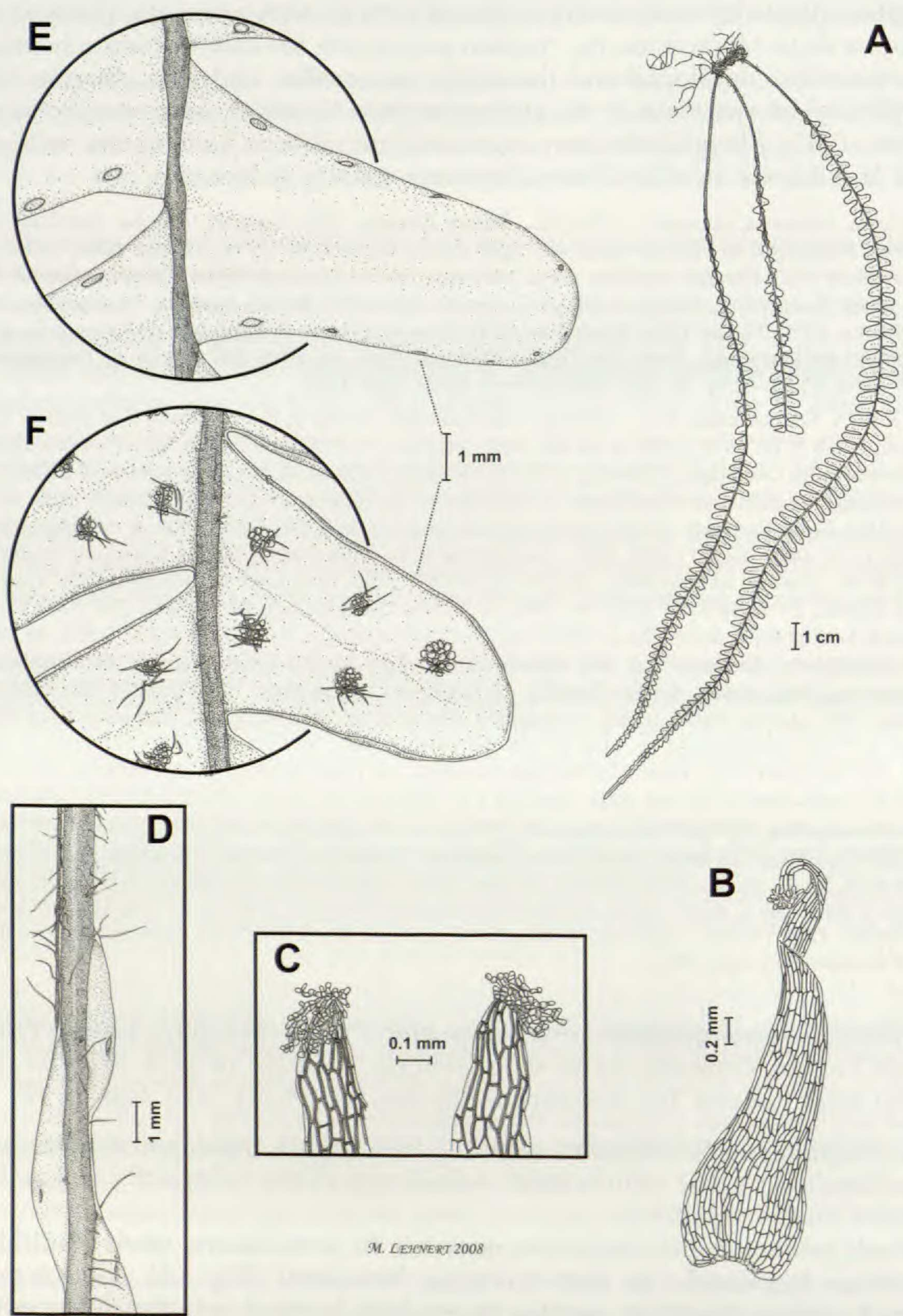
ADDITIONAL SPECIMENS EXAMINED.—BRAZIL. **Minas Gerais:** Alto Caparaó, Parque Nacional do Caparaó, along trail to Pico da Bandeira, 2600 m, ca. 20°31'S, 41°53'W, 21 Mar 1999, *Salino & Moraes 4538* (UC). **Paraná:** Curitiba, Serra Ibitiraque, Morro Camapuã (Mun. Campina Grande do Sul), 25°08'S, 49°04'W, 02 Mar 2000, *Ribas et al. 3080* (UC). **Rio de Janeiro:** Teresópolis, ca. 22°25'S, ca. 42°58'W, Oct 1929, *Brade 9094* (NY); boundary between município de Teresópolis and Município de Petrópolis, Serra dos Orgãos National Park, ca. 5 km SW of city of Teresópolis, 22°27–28'S, 43°01–02'W, 30 Nov 1965, *Eiten & Eiten 7168* (US).

BOLIVIA. **Cochabamba:** Prov. Ayopaya, San Cristobal, climbing along the trail that leads to San Miguel, 16°39'S, 66°43'W, 3100 m, 06 Jun 2002, *Jiménez I. 1107B* (GOET, LPB, UC); Prov. Carrasco, on the way from Comarapa to Siberia, 17°50'S, 64°42'W, 3000 m, 22 Jan 2000, *Jiménez I. 283* (LPB, UC); 10 km from Siberia to Comarapa, 17°48'S, 64°42'W, 2600 m, 20 Oct 1996, *Kessler et al. 9164* (LPB, UC); Prov. Carrasco, 10 km Cocapata-Cotacajes, 16°38'S, 66°41'W, 3000 m, 09 May 1997, *Kessler et al. 9401* (GOET, LPB, UC); road Cochabamba-Villa Tunari, below Corani, 17°10.58'S, 65°53.67'W, 2700 m, 26 Nov 2002, *Lehnert 512* (GOET, LPB, UC); road Cochabamba-Villa Tunari, below Corani, 17°10.58'S, 65°53.67'W, 2700 m, 26 Nov 2002, *Lehnert 514* (GOET, LPB, UC); Prov. Chapare, Cochabamba 54 km hacia Villa Tunari, 2750 m, 30 Apr 1979, *Beck 1424a* (LPB). **La Paz:** Prov. Inquisivi, "Kinpayá," at the mouth of the Río Jancha Kaihua where the Aquilani-Choquetanga trail crosses the Río Ocsalla, 10 km N of Choquetanga, 16°45'S, 67°17'W, 3400 m, 07 Sep 1991, *Lewis 39952* (LPB); comunidad Choquetanga-Wichupampa, Serranías de Lulini 13 km al N de Choquetanga, 2–3 km al NW del cerro Lulini, 16°45'S, 67°20'W, 3290 m, 17 Mar 1994, *Salinas 2783* (US); Prov. Nor Yungas, Coscapa, on prehispanic trail Sillutinkara, 16°12'S, 67°53'W, 3100–3300 m, 07 Jan 2001, *Jiménez I. & Vidaurre 526* (LPB, UC), 559 (GOET, LPB, UC); Unduavi, trench to the Valle de Coscapa, 16°17'S, 67°51'W, 3350 m, 04 Feb 2003, *Lehnert 599, 601, 602* (GOET, LPB, UC). **Santa Cruz:** Prov. Caballero, Comarapa, between Torecillos and Siberia, 17°49.65'S, 64°40.14'W, 2600–2700 m, 18 Mar 2003, *Lehnert 696, 707* (GOET, LPB, UC); from Siberia 4 km to the E, small laguna on the ridge (Laguna Tinqué?), 2600 m, 18 Mar 2003, *Lehnert 717* (GOET, LPB, UC); by small lake at summit of pass ca 4 km E of Siberia, 2800 m, 04 Jan 2000, *Wood & Goyder 15792* (LPB).

***Melpomene caput-gorgonis* Lehnert, sp. nov.** TYPE.—BOLIVIA. **La Paz:** Prov. Nor Yungas, Cotapata, detras del gasolinero, 3200 m, 16°17'S, 67°51'W, 25 Sep 2002, *Lehnert 367* (holotype: LPB; isotypes: GOET, UC). **Figs. 2, 7B.**

A *Melpomene flabelliformi* petiolis brevioribus, apicibus squamarum latoribus (3–4 vs. 1–2 cellulis latis), cellulis apicalibus creberioribus, absentia pilorum inter soros differt.

Plants predominantly epiphytic, growing in moss layers, rarely epilithic. *Rhizomes* moderately to short-creeping, horizontal (Fig. 2A), 1.0–1.5 mm diam. *Fronde*s to 35–42 cm, arching to pendent, inserted onto the rhizomes at right angles (Fig. 2A), closely arranged (internodes 1–4 mm). *Scales* to 6.5×0.8 –1.0 mm, (18–)20–26(–32) cells wide, clathrate, auburn to brown, strongly iridescent, broadly cordate to pseudopeltate, with obtuse to truncate tips ending in rows of 3–4 cells (Fig. 2B); apical cells numerous, sitting clustered on the wide tips (Fig. 2C). *Petioles* 15–50(–70) mm long, 0.6–0.8(–1.0) mm



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FIG. 2. *Melpomene caput-gorgonis*: A. habit (Kessler 1192, GOET); B. scale (Lehnert 868, GOET); C. detail of scale apices (Jiménez I. 534, LPB); D. petiole, upper part adaxially (Lehnert 868, GOET); E. segment adaxially (Lehnert 868, GOET); F. fertile segment abaxially (Lehnert 868, GOET).

thick, decurrently marginate from the laminar bases, with brown flaccid ciliform hairs (1.0–2.0 mm) on both sides (Fig. 2D), simple and branched clavate hairs of crosiers and young fronds sometimes persistent in older fronds, but generally glabrescent. *Laminae* firm-chartaceous, rarely coriaceous (*Lehnert* 781), to $300(-350) \times 14-22$ mm, narrow-elliptic (broadest in the middle), decurrent at bases, acute to attenuate at tips, sometimes caudate (Fig. 2A). *Rachises* dark brown, flat, and slightly sunken between segments adaxially (Fig. 2E), weakly hemispherically protruding abaxially (Fig. 2F), glabrous except for the proximal part, with ciliform hairs as on petioles. *Segments* $4.5-9.0(-12.0) \times 3.2-3.8(-5.0)$ mm (1.5–3 times longer than broad), weakly ascending ($80-70^\circ$), oblong to lunate, equilateral at bases or weakly basiscopically decurrent, fully adnate, the tips obtuse to round (Fig. 2E, F); midveins not visible, or obscurely so abaxially (Fig. 2F), especially in dried specimens; proximal pairs markedly smaller than the central segments (Fig. 2A), inequilateral at bases, basalmost auriculiform (e.g., *Lehnert* 368), but never trapezoid; rarely few ciliform hairs scattered along the segment margins; hydathodes present (Fig. 2E). *Sori* 2–4 pairs per segment, with 3–10 receptacular and circumsoral ciliform hairs 1.0–1.5 mm long (Fig. 2F).

The name refers to the numerous apical cells on the scale tips; these cells resemble the head of Medusa, one of the Gorgons in Greek mythology, which had snakes instead of hair (Latin, *caput* = head).

Melpomene caput-gorgonis grows in wet montane forests and elfin forests at 2680–3200 m in southern Peru and Bolivia (Fig. 7B).

The most distinguishing feature of this species is the broad scales with the abundant apical papillae. No other species of *Melpomene* has scale apices that provide a base for papillae several cells wide. *Melpomene flabelliformis* can be distinguished from *M. caput-gorgonis* by its distant fronds and glabrous or glabrescent petioles (vs. fronds close and petioles persistently hairy in *M. caput-gorgonis*). *Melpomene flagellata* is generally more slender in habit and most features, i.e., laminae to 9(–16) mm wide (vs. to 22 mm), rhizomes thinner and ascending, petiole scales narrower, and hairs in the sori longer.

Melpomene caput-gorgonis grows together with *M. paradoxa*, which can be distinguished by its longer, glabrescent petioles and shorter segments; the latter species also forms patches with the fronds erect to arching whereas *M. caput-gorgonis* grows solitary with arching to pendent fronds.

ADDITIONAL SPECIMENS EXAMINED.—PERU. **Cuzco:** Abra de Chaupimayo, Hacienda Pintubamba, 2700 m, Sep 1932, *Bües* 1945 (CUZ).

BOLIVIA. **La Paz:** Prov. Franz Tamayo, PN-ANMI Madidi, trail Keara-Mojos, below Chunkani, 2870 m, $14^\circ38'S$, $68^\circ57'W$, 08 Nov 2001, *Jiménez I. & Gallegos* 917 (LPB, UC); Prov. Larecaja, toll house above Mapiri, 2000 m, 12 Sep 1901, *Williams* 1154 (NY); Prov. Nor Yungas, Estación Biológica Tunquini, Bajo Hornuni, senda del campo de Don Pedro al camino de la mina, 2550 m, $16^\circ11'S$, $67^\circ53'W$, 17 Aug 2000, *Jiménez I. et al.* 488 (LPB, UC); Coscapa, along the prehispanic trail Sillutinkara, $16^\circ12'S$, $67^\circ53'W$, 3100 m, 07 Jan 2001, *Jiménez I. & Vidaurre* 534 (LPB, UC); trench to the Coscapa valley, Parque Nacional Cotapata, $16^\circ12'S$, $67^\circ33'W$, 3000 m, 12 Dec 1997, *Kessler et al.* 1871 (LPB); 2 km from Chuspipata to Coroico, $16^\circ22'S$, $67^\circ49'W$, 2900 m, 19 Sep 1997, *Kessler et al.* 11921 (GOET, LPB, UC); Cotapata, behind the gas station, $16^\circ17'S$, $67^\circ51'W$, 3150–3200 m, 25 Sep 2002, *Lehnert* 367, 368, 369, 372, 373, 386, 392 (GOET, LPB, UC); Chuspipata-

Sacramento, 16°18'S, 67°49'W, 2680 m, 10 Nov 2002, *Lehnert 496a* (GOET, LPB, UC); 1.2 km E de Cotapata-Santa Barbara, trail to the Chuspipata electricity station, 16°17'S, 67°50'W, 3200 m, 02 Feb 2003, *Lehnert 586* (GOET, LPB, UC); Chuspipata, old trail to Unduavi, 3200 m, 07 May 2003, *Lehnert 781* (GOET, LPB, UC).

Melpomene flagellata Lehnert, *sp. nov.* TYPE.—BOLIVIA. **La Paz:** Prov. Nor Yungas, N side of Cerro Uchumachi above Coroico, 16°12'S, 67°45'W, 2350 m, 14 Jul 1989, *Kessler & Kelschbach 107* (holotype LPB; isotype GOET). **Figs. 3, 7C.**

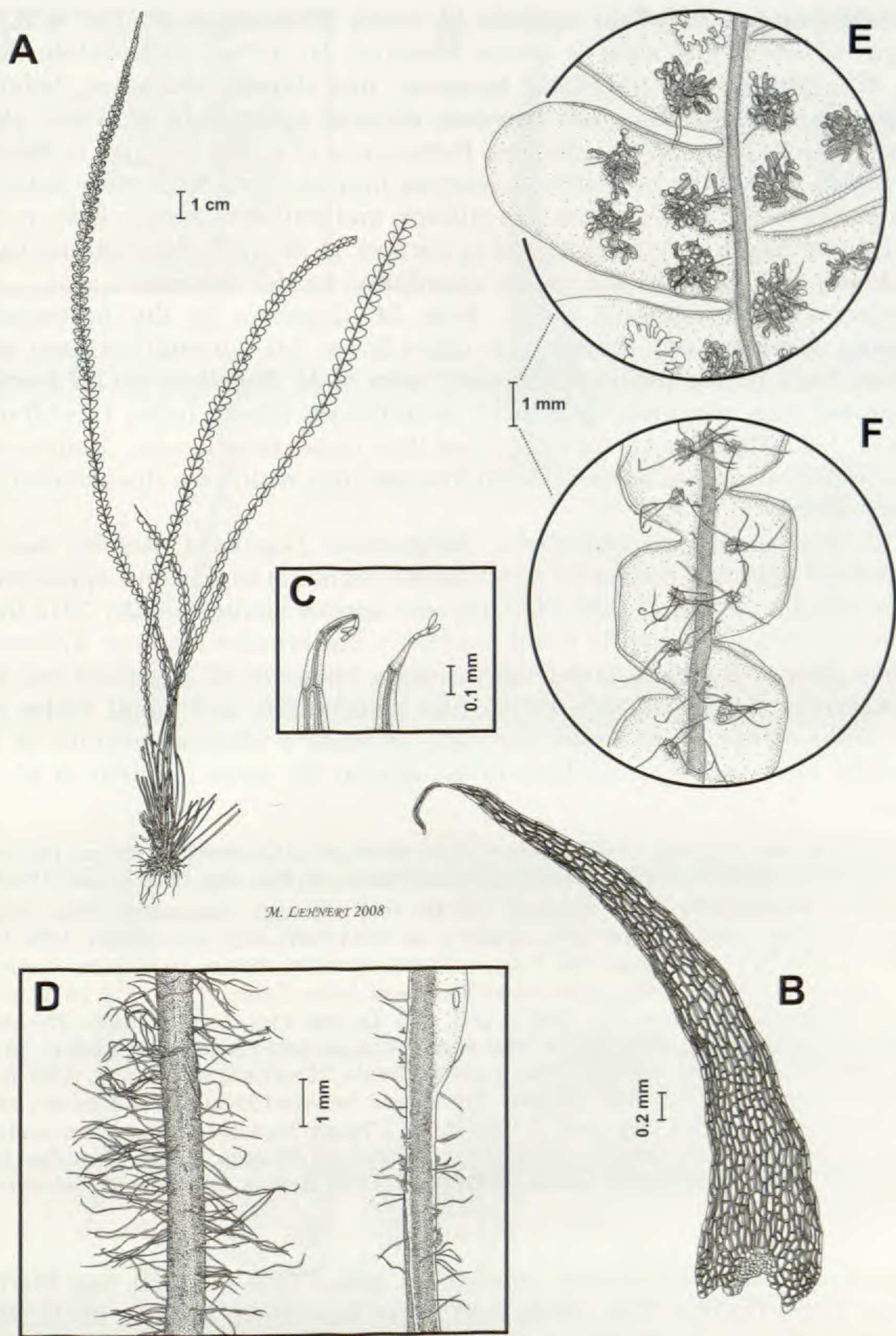
A *Melpomene moniliformi* pilis longioribus (1.0–2.0 mm vs. 0.5–1.0 mm), crebrioribus in petiolis sorisque, rhizomatibus ascendentibus (vs. horizontaliter reptantibus) apicibusque segmentorum partim truncatis (vs. semper obtusis vel rotundis) differt.

Plants predominantly epiphytic, growing in moss layers, sometimes epilithic. *Rhizomes* erect or ascending, short to moderately long (Fig. 3A), 0.8–1.0(–1.5) mm diam. *Fronds* to 38 cm long, erect, inserted onto the rhizome at acute angles, closely arranged (internodes 1–5 mm), but not caespitose (Fig. 3A). *Scales* 3.0–5.0 × 0.5–0.6 mm, 12–16(–20) cells wide, clathrate (Fig. 3B), dark brown to brown, strongly iridescent, cordate to pseudopeltate, acute to attenuate at tips (Fig. 3C); apical cells 3–8, as furcate hairs or palmately arranged. *Petioles* 15–60(–75) mm long (Fig. 3A), (0.4–)0.5–0.6(–0.8) mm thick, decurrently marginate from the laminar bases, most parts terete (Fig. 3C), with many brown, setiform and ciliform hairs 1.0–2.0 mm long (Fig. 3C), simple and branched clavate hairs of crosiers and young fronds sometimes persistent in older fronds. *Laminae* firm-chartaceous, 150–320 × 4–9(–16) mm, linear to narrow-elliptic (broadest in the middle), long-decurrent at base, acute to attenuate at tip. *Rachises* dark brown to black, planar and slightly sunken between segments adaxially, hemispherically protruding abaxially (Fig. 3D), glabrous or glabrescent with branched clavate hairs distally, usually sparsely to densely hairy basally on both sides with ciliform and setiform hairs like on the petioles. *Segments* 1.8–3.0(–4.0) × 1.4–3.0 mm (1–2 times longer than broad), ascending (80–55°), fully adnate, inequilateral at bases, basiscopically decurrent, most segments lunate to deltate with the tips obtuse to truncate (Fig. 3E), sometimes distal segments short-oblong with round tips (Fig. 3D); proximal segment pairs markedly smaller than the central segments, trapezoid with truncate tips, often auriculiform; midveins not visible (Figs. 3D, E), or obscurely so abaxially in dried specimens; segments glabrous except for hairs in sori; margins without hairs; hydathodes present. *Sori* 2–4 pairs per segment, with (3–)12–20 hairs 1.2–1.8 mm long (Figs. 3D, E), rarely some sori of a frond without hairs.

The name refers to the narrow laminae with long curved tips, which are reminiscent of whips (Latin, *flagellum*).

Melpomene flagellata occurs in elfin forests and moist montane forests at 1950–3300 m in eastern Peru and Bolivia (Fig. 7C).

The segment shape of *Melpomene flagellata* varies strongly between trapezoid to rounded in small segments to deltate or short-oblong in larger



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FIG. 3. *Melpomene flagellata*: A. habit (Kessler & Kelschbach 107, GOET); B. scale (Kessler & Kelschbach 107, GOET); C. detail of scale apices (Kessler & Kelschbach 107, GOET); D. petiole, left central part, right upper part (Lehnert 517, GOET); E. oblong segments abaxially, sporangia mature and open (Kessler et al. 7138, LPB); F. truncate segments abaxially, sporangia primordial (Kessler & Kelschbach 107, GOET).

ones. *Melpomene flagellata* replaces *M. wolfii* (Hieron.) A. R. Sm. & R. C. Moran, which at first sight is almost identical, in Bolivia and eastern Peru (Fig. 7C). *Melpomene flagellata*, however, has thinner rhizomes, thinner petioles with thinner alae, and narrower rhizome scales than *M. wolfii*; also, *M. wolfii* lacks hairs on the petioles. Pubescence of fertile laminae is similar and highly variable in both species, varying from glabrous to densely hairy in even one plant. In *M. flagellata*, the ciliform and setiform laminar hairs reach 1.2–1.8 mm length and are clustered in the sori; in *M. wolfii*, the laminar hairs are shorter (0.5–0.8 mm) and evenly distributed on the laminae.

Melpomene moniliformis differs from *M. flagellata* in the horizontally creeping rhizomes and shorter (0.5–1.0(–1.5) vs. 1.0–2.0 mm) setiform and ciliform hairs on the petioles. The soral hairs of *M. flagellata* are on average longer and more abundant than in *M. moniliformis* (12–20 hairs, 1.2–1.8 mm long vs. 1–5 hairs, 0.5–1.0 mm long) and thus more conspicuous. *Melpomene moniliformis* also lacks segments with truncate tips, which are characteristic of *M. flagellata*.

With the mentioned characters, *Melpomene flagellata* can be readily determined although it shows a considerable variation in size and appearance within its small range. *Kessler 7320* has very narrow blades; *Kessler 7318* from the same location is equal in frond length but has broader laminae; *Krömer & Acebey 1368* is generally larger than average plants of *M. flagellata* but has characteristic short segments, fitting hair distribution, and small scales (16 cells wide across base). Molecular data indicate a stronger affinity of *M. flagellata* to *M. moniliformis* than to the similar *M. wolfii* (Lehnert *et al.*, in press).

ADDITIONAL SPECIMENS EXAMINED.—PERU. **Cuzco:** Alturas de Sicre, La Convención, 3000 m, Jun 1924, *Bües 1574* (CUZ). **Puno:** Sachapata, Ostabhang der Cordilleren von Peru, Sep 1854, *Lechler 2713* (B).

BOLIVIA. **Cochabamba:** Prov. Carrasco, 132 km [on] old road Cochabamba-Villa Tunari, 17°06'S, 65°35'W, 1950 m, 15 Jul 1996, *Kessler et al. 7318* (LPB, UC), *7320* (GOET, LPB, UC); 130 km [on] old road Cochabamba-Villa Tunari, 17°07'S, 65°36'W, 2000 m, 10 Jul 1996, *Kessler et al. 7168* (GOET, LPB, UC); road Cochabamba-Villa Tunari, below Corani, 17°10.51'S, 65°54.02'W, 2750 m, 26 Nov 2002, *Lehnert 517* (GOET, LPB, UC). **La Paz:** Prov. Franz Tamayo, PN-AMNI Madidi, trail Keara-Mojos, about half an hour from Tokuaque, 14°37'S, 68°57'W, 2420 m, 01 Jul 2001, *Jiménez I. & Gallegos 527* (UC); Prov. Larecaja, Sorata, 15°44.04'S, 68°39.28'W, 3300 m, 06 Jan 2003, *Lehnert 555* (GOET, LPB, UC); Prov. Nor Yungas, between Chuspipata and Yolosa, above Sacramento, 2760 m, 01 Jan 1994, *Beck 21310* (LPB, UC); Parque Nacional Cotapata, surroundings of Estación Biológica Tunquini, 16°11'S, 67°52'W, 2300 m, 26 Jul 2000, *Krömer & Acebey 1368* (GOET, LPB, UC); Chuspipata–Sacramento, 16°18'S, 67°49'W, 2900 m, 10 Nov 2002, *Lehnert 491* (GOET, LPB, UC).

***Melpomene huancabambensis* Lehnert, *sp. nov.* TYPE.** — PERU. **San Martin:** Prov. Rioja, Buenos Aires, along road Pedro Ruiz-Rioja, 2000 m, 05°42'09"S, 77°53'06"W, *van der Werff et al. 15352* (holotype: UC; isotype: MO). **Figs. 4, 7D.**

A *Melpomene pilosissima* (M. Martens & Galeotti) A. R. Sm. & R. C. Moran absentia vel praesentia irregulari hydathodorum, a *M. michaeli*, *M. xiphopteroides* et *M. jimenezii* pilis in paginis laminarum abaxialibus aequaliter distributis (vs. in soris confertis) differt.

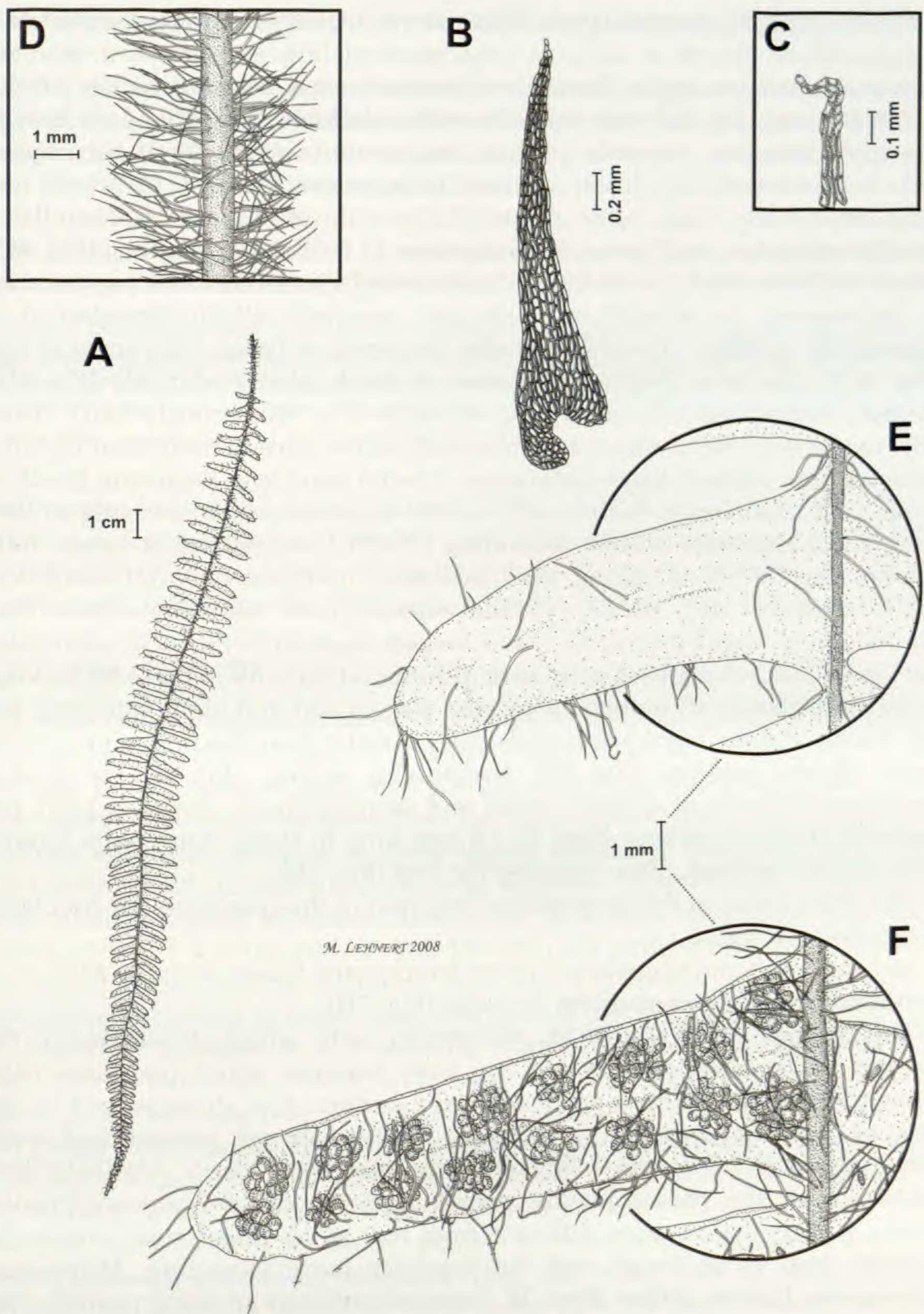


FIG. 4. *Melpomene huancabambensis*: A. frond; B. scale; C. detail of scale apex; D. petiole, central part; E. segment adaxially; F. segment abaxially, sporangia immature (all from van der Werff et al. 15353, UC).

Plants epiphytic in moss layers. *Rhizomes* stout, very short-creeping to erect, 1.0 mm diam. *Fronde*s to 33.5 cm long, pendent (Fig. 4A), inserted onto the rhizomes at narrow angles, fasciculate (internodes 0.2–1.0 mm). *Scales* 2.0–3.2 \times 0.3–0.5 mm, (10–)12–14(–16) cells wide, clathrate (Fig. 4B), dark brown, strongly iridescent, narrowly cordate, long-acute to attenuate at tips; apical cells 3–5, in a nodding cluster or linear arrangement. *Petioles* (12–)45–55 mm long, 0.6–1.0 mm thick, terete, densely hairy with setiform and ciliform hairs, usually rather lax, dark brown to castaneous, (1.8–)2.0–3.5 mm long (Fig. 4C); simple and branched clavate hairs absent or very sparse. *Laminae* papyraceous to chartaceous, to 140–290 \times 29–36 mm, narrowly elliptic (broadest at or beyond the middle), cuneate to shortly decurrent at bases, long-acute at tips (Fig. 16A). *Rachises* deeply dark brown to black, planar adaxially (Fig. 4D), strongly hemispherically protruding abaxially (Fig. 4E), strongly hairy abaxially, moderately hairy adaxially, proximally more densely hairy than distally, setiform and ciliform hairs castaneous, 1.5–3.0 mm long. *Segments* 22–28 \times 8 mm (3–4 times longer than broad), central segments patent or nearly so (90–80°), distal segments weakly ascending (75–65°), equilateral at bases, fully adnate, long-deltate to oblong, the tips obtuse; midveins obscurely visible in dried specimens (Fig. 4D, E); proximal segment pairs markedly smaller than the following segments (1/2 to 1/3 of longest segments) (Fig. 4A), sometimes the lowermost 2–5 segment pairs auriculiform; setiform hairs 1.0–2.0 mm long, evenly distributed on laminae abaxially, also in sori and along midveins but not clustered here, hairs present adaxially mainly along the midveins, always some on the margins (Fig. 4E); hydathodes lacking (Fig. 4D) or weakly developed in parts of a frond, small and inconspicuous. *Sori* 3–9 pairs per segment, (0–)1–3 setiform hairs to 1.5 mm long in them, more hairs around them on the laminae, often covering the sori (Fig. 4E).

The name refers to the geographic restriction of the species to the Amotape-Huancabamba region.

Melpomene huancabambensis grows in montane forests at 1900–2200 m in northeastern Peru and southern Ecuador (Fig. 7D).

This species is an ally of *M. pilosissima*, with which it matches in the densely hairy, terete petioles and the hairy laminae, which may have hairs along the segment margins and the adaxial surface. It is characterized by the lack or poor development of hydathodes (vs. always present and well-developed in *M. pilosissima*). The often large size of the plants, relatively short petioles, and the predominantly patent segments of *M. huancabambensis* create a habit that is quite different from that of *M. pilosissima*, where the petioles tend to be longer and the segments more ascending. *Melpomene pilosissima* further differs from *M. huancabambensis* in being usually less hairy on the segments adaxially; however, there are some exceptions. Some plants of *M. pilosissima* are equal to *M. huancabambensis* in the hairiness of the adaxial segment surfaces, but tend to have more acute segment tips, discontinuously visible midveins, and decurrently marginate petioles (all characters not present in *M. huancabambensis*).

Melpomene vernicosa (Copel.) A. R. Sm. & R. C. Moran and larger plants of *Melpomene xiphopteroides* are superficially similar to *M. huancabambensis* but they differ in having hairs clustered in the sori (vs. not clustered in sori in *M. huancabambensis*). *Melpomene vernicosa* also has glabrous segment margins (vs. hairy in *M. huancabambensis*) and more coriaceous laminae (vs. papyraceous to chartaceous). Other species with absent or weakly developed hydathodes (*M. jimenezii*, *M. michaelis*), which are characteristic of *M. huancabambensis*, differ in having ascending segments, more coriaceous laminae, and hairs clustered in the sori.

ADDITIONAL SPECIMENS EXAMINED.—ECUADOR. **Zamora-Chinchipe:** P.N. Podocarpus, park entrance “San Francisco,” on new Loja-Zamora rd., 03°59.349'S, 79°05.713'W, 2151 m, 14 Dec 2006, Sundue 1123 (NY, UC). PERU. **San Martin:** Prov. Rioja, along road Pedro Ruiz-Rioja, 05°42'09"S, 77°53'06"W, 2000 m, 21 Mar 1998, van der Werff *et al.* 15353 (MO, UC); *ibid.*, El Mirador, 1900 m, 26 Mar 1998, van der Werff *et al.* 15749 (MO, NY, UC).

***Melpomene jimenezii* Lehnert, *sp. nov.* TYPE.**—BOLIVIA. **La Paz:** Prov. Franz Tamayo, Parque Nacional Madidi, trail Pelechuco-Mojos, locality Tambo Quemado (camping area), on the trail towards Qalla, crossing the fourth river and going up the trail which leads through the *Polylepis* forest, 14°41'S, 68°58'W, 3490 m, Jiménez I. 1859 (holotype: LPB; isotypes: GOET, UC). **Figs. 5A–D, 7D.**

A *Melpomene pilosissima* absentia hydathodorum (vel hydathodibus sparse et irregulariter praesentibus vs. semper praesentibus *M. pilosissima*), a *M. michaeli* squamis maioribus (usque 5.5–7.5 vs. 2.0–3.0 mm longis), pilis inter soros sparse distributis vel carentibus (vs. pilis crebris inter soros) praestans.

Plants epiphytic, growing in moss layers. *Rhizomes* short-erect (Fig. 5A), 1.2–1.8 mm diam. *Fronds* to 35 cm long, pendent, inserted onto rhizomes at acute angles, closely arranged (internodes 1–4 mm), caespitose (Fig. 5A). *Scales* 5.5–7.5 × 0.4–0.6 mm, (8–)14–18(–20) cells wide across base, clathrate (but usually many lumina occluded), dark brown to brown, weakly iridescent, subcordate to cordate at bases, long attenuate at tips (Fig. 5B); apical cells 5–12, palmately arranged or in a nodding cluster (Fig. 5C). *Petioles* 40–80 mm long, 0.8–1.0 mm diam., terete, with many dark brown setiform and ciliform hairs 1.2–3.0 mm long (Fig. 5A), simple and branched clavate hairs of crosiers and young fronds persistent on older fronds. *Laminae* 205–285 × 30–64 mm, coriaceous, adaxially matte, lanceolate or broadly elliptic (broadest at or below the middle), acute to attenuate at tips, bases rounded to cuneate (Fig. 5A). *Rachises* dark brown to black, planar to weakly protruding adaxially, hemispherically protruding abaxially (Fig. 5D), with few to many brown setiform and ciliform hairs on both sides (1.0–1.5 mm), usually hairier abaxially than adaxially; abaxially also with many simple and branched hairs. *Segments* 18.0–35.0 × 2.8–4.0 mm (6–12 times longer than broad), patent to weakly ascending (80–60°), fully adnate, equilateral at bases, or weakly decurrent towards the blade apices, tips obtuse (Fig. 5A); proximal segment pairs oblong to deltate, smaller than the following segments, but not

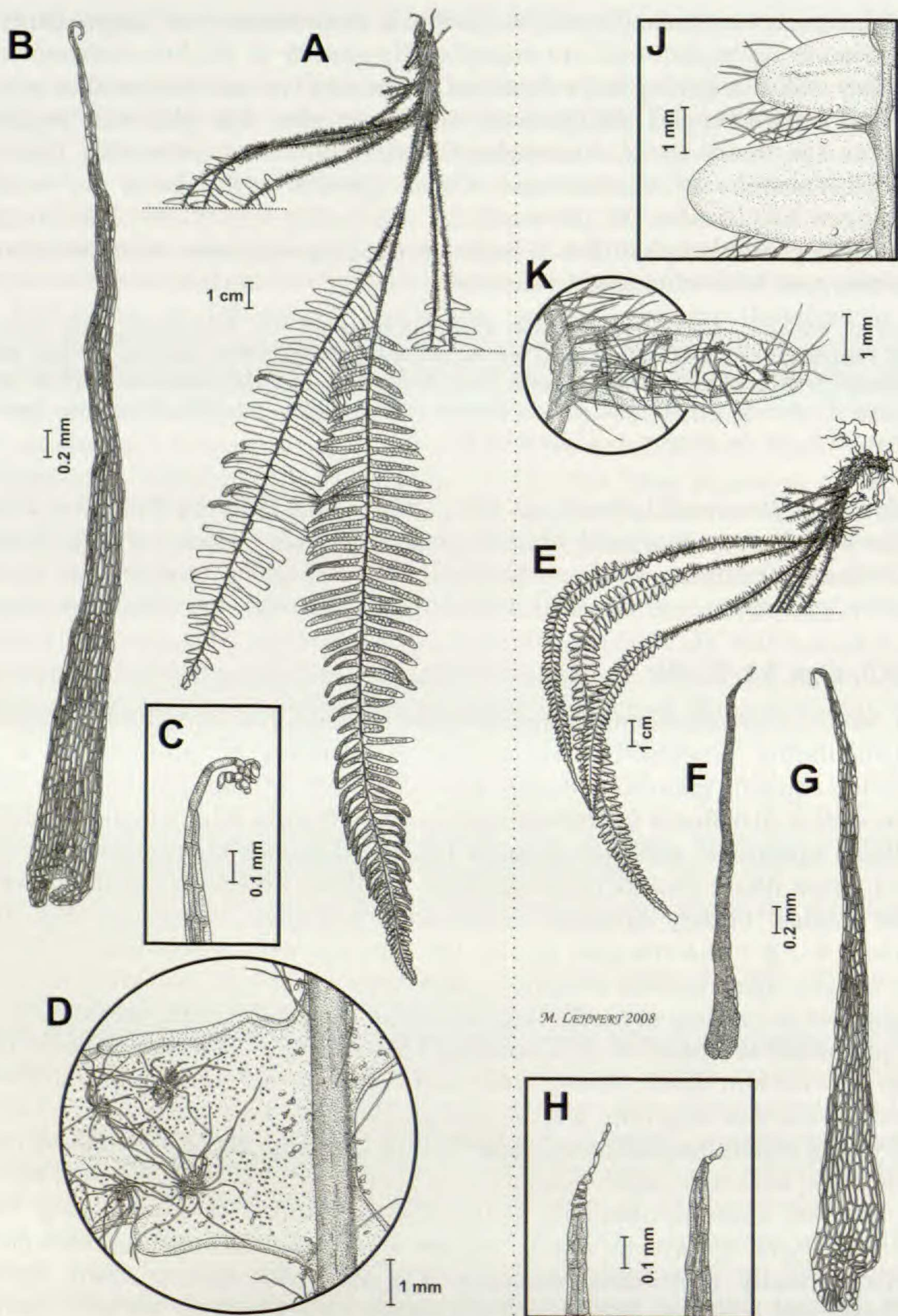


FIG. 5. *Melpomene jimenezii* (A–D): A. habit; B. scale; C. detail of scale apex; D. segment abaxially, sporangia removed (all from Jiménez I. 1859, GOET). *Melpomene michaelis* (E–J): E. habit; F. scale, with unexpanded cells; G. scale, typical; H. detail of scale apices; I. basal segments adaxially; J. basal segments adaxially; K. fertile segment abaxially, sporangia primordial (all from Lehnert 443, GOET, except for F, Lehnert 519, GOET).

auriculiform, often remote; margins entire or dentate basally in large segments (Fig. 5D), fertile segments often conduplicate; midveins not visible on both laminar sides, or obscurely so abaxially in dried specimens; stomata usually visible as dark brown to reddish dots (Fig. 5D); setiform/ciliform hairs to 2 mm long, clustered in sori, lacking or sparse along midveins or on laminae abaxially, margins and adaxial laminar surface glabrous (Fig. 5D); hydathodes usually absent, sometimes weakly developed in some parts of a frond. *Sori* 3–10 pairs per segment, each with 4–10 ciliform hairs (0.8–1.5 mm).

The species is named after Ivan Jiménez, Bolivian botanist and colleague, who collected the type specimen.

Melpomene jimenezii grows in elfin forest and moist montane forests at 2400–3800 m in Peru and Bolivia (Fig. 7D).

This species is remarkable because it lacks conspicuous hydathodes in most fronds. Occasionally, some segments have small hydathodes, while hydathodes are otherwise absent on the same frond. Other species with such irregular development of hydathodes are *M. huancabambensis* and *M. michaelis*. According to Parris (1997), absence and presence of hydathodes may change in many grammitid taxa in the Paleotropics, but until now it has been considered a reliably constant feature for the Neotropical genera.

The prevailing lack of hydathodes separates *M. jimenezii* from the superficially similar *M. firma*, which always has well developed hydathodes and also differs in having conspicuous black midveins (vs. midveins not visible or obscure in *M. jimenezii*) and fewer, shorter hairs on the petioles (vs. densely long-hairy).

From *Melpomene pilosissima*, *M. jimenezii* differs in having longer segments, ciliform hairs clustered in the sori (vs. evenly distributed on the laminae), and in lacking setiform or ciliform hairs along the margins and the adaxial laminae (vs. regularly hairy along the margins and the adaxial laminae). The smaller *M. michaelis* is similar, but differs from *M. jimenezii* by having setiform and ciliform hairs on the laminae between the sori (vs. restricted to the sori), lacking red stomata (vs. stomata often red), and having rhizome scales about half the size of those of *M. jimenezii* (2.0–3.0 vs. 5.5–7.5 mm long).

ADDITIONAL SPECIMENS EXAMINED.—PERU. **Amazonas:** Leimebamba, 2400 m, 30 Dec 1962, *Woytkowski* 7839 (UC). **Pasco:** Prov. Oxapampa, Huancabamba district, locality Lanturachi, sector Santa Bárbara, 10°21'S, 75°39'W, 3800 m, 10 Oct 2003, *Perera et al.* 531 (MO, USM).

BOLIVIA. **La Paz:** Prov. Franz Tamayo, PN-ANMI Madidi, senda Pelechuco-Mojos, por el sendero que va hacia Qalla, cruzando el 4° río y subiendo por el sendero que atravieza el bosque de *Polylepis*, 14°41'S, 68°58'W, 3360 m, 03 May 2003, *Jiménez I.* 1842A (LPB, UC); *ibid.*, localidad Tambo Quemado (lugar para acampar), 3250 m, 14°39'S, 68°57'W, 04 May 2003, *Jiménez* 1891 (LPB, UC).

Melpomene michaelis* Lehnert, *sp. nov.* TYPE. — BOLIVIA. **Cochabamba:** Prov. Carrasco, carretera Cochabamba-Villa Tunari, debajo de Corani, 2750 m, 17°10.51'S, 65°54.02'W, *Lehnert* 519 (holotype: GOET; isotypes: LPB, UC). **Figs. 5E–K, 7D.*

A *Melpomene pilosissima* pilis in soris confertis, hydathodis partim reductis, a *M. jimenezii* squamis minoribus (usque 2.0–3.0 vs. 5.5–7.5 mm longis), pilis crebris inter soros (vs. pilis inter soros sparse distributis vel carentibus) differt.

Plants predominantly epilithic, also epiphytic. *Rhizomes* very short-creeping (Fig. 5E), ascending to erect, 0.8–1.4 mm diam., rarely branched. *Fronds* to 18 cm long, rather laxly pendent, inserted onto the rhizomes at acute angles, closely arranged (internodes 0.2–1.0 mm), caespitose (Fig. 5E). *Scales* to 2.0–3.0 × 0.4–0.6 mm, (8–)10–12(–16) cells wide across base, clathrate (Fig. 5F), dark brown to brown, weakly iridescent, narrowly lanceate, narrowly cordate basally, attenuate at tips; apical cells 1–8, linearly arranged (Fig. 5H); sometimes cells of scales unexpanded, then scales blackish and not iridescent (Fig. 5G). *Petioles* 26–55 mm long, 0.4–0.6 mm diam., terete, with many dark brown, setiform and ciliform hairs 1–3 mm long; simple and branched clavate hairs of crosiers and young fronds sometimes persistent on older fronds. *Laminae* to 115–125 × 11–20 mm (2/3 of frond length), firm-chartaceous, adaxially usually shiny, narrowly elliptic to linear-elliptic (widest at and/or below the middle), round to broadly cuneate at bases, short-attenuate to acute at tips (Fig. 5E). *Rachises* dark brown to black, planar and slightly sunken between segments adaxially, hemispherically protruding abaxially, densely hairy as on petioles abaxially and in the proximal half adaxially. *Segments* 4.5–7.2 × 1.4–2.2 mm (2.5–3.0 times longer than broad), weakly ascending (80–75°), inequilateral at bases, fully adnate, long-deltate to oblong, the tips obtuse (Figs. 5J, K); midveins not visible, or obscurely so abaxially in dried specimens; proximal 1–3 segment pairs markedly smaller than the following segments, but not auriculiform; few to many setiform and ciliform hairs 1–2 mm long on the abaxial laminar surface, clustered in and around sori, always some along the margins, rarely some adaxially; stomata not visible as dark spots; hydathodes small, inconspicuous and regularly lacking in some parts of the fronds (Fig. 5J). *Sori* 1–6 pairs per segment, with 1–3 long setiform and ciliform hairs 1.5–2.0 mm long (Fig. 5K).

The name honors both Michael Kessler, my mentor at Göttingen University, and Michael Sundue, a colleague from New York Botanic Garden, who first recognized this species as being distinct.

Melpomene michaelis grows in wet montane forests at 2250–3450 m in Peru and Bolivia (Fig. 17A).

A noteworthy character of *Melpomene michaelis* is the inconspicuous, sometimes partially absent hydathodes. In gross morphology, *M. pilosissima* is virtually identical to *M. michaelis*, but has always well-developed hydathodes and evenly distributed setiform/ciliform hairs on the abaxial laminar surface; there may be few hairs present in the sori, but they are not clustered here like it is the case in *M. michaelis*. *Melpomene pilosissima* occurs in Mesoamerica and the northern Andes and shows no geographical overlap with *M. michaelis*, which is confined to the central Andes. Ecologically, *Melpomene michaelis* prefers the epilithic habitat whereas *M. pilosissima* is mainly found as an epiphyte.

The distribution of *Melpomene michaelis* overlaps with that of *M. jimenezii*, which—like *M. michaelis*—has setiform/ciliform hairs clustered in the sori. Apart from the larger size, *M. jimenezii* differs in having longer, more linear segments than *M. michaelis* and in lacking hydathodes, or having occasionally small hydathodes in some segments (vs. hydathodes inconspicuous but predominantly present in *M. michaelis*). It also lacks hairs between the sori on the abaxially laminar surface (vs. sparsely to densely hairy between the sori in *M. michaelis*), on the segments margins, and adaxial laminar surface (vs. sometimes with scattered hairs on margins and adaxial laminar surface).

A peculiar trend is observed in the rhizome scales of *M. michaelis*: already having scales with smaller cells than in most *Melpomene* species on average, the cells in the southern populations are often not expanded, with thick cell walls occluding the usually translucent lumina.

ADDITIONAL SPECIMENS EXAMINED.—PERU. **Cuzco**: Prov. Urubamba, Machu Picchu, along trail from Machu Picchu ruins to Wiñay Waina, 2300 m, 21 Jan 1976, *Bishop 2513* (UC); entre San Luis y Abra Málaga, 13°06.22'S, 72°22.42'W, 3450 m, 16 Oct 2002, *Lehnert 443* (GOET, UC, USM).

BOLIVIA. **Cochabamba**: Prov. Ayopaya, San Cristobal, subiendo por el sendero que va a San Miguel, 16°39'S, 66°43'W, 3250 m, 06 Jun 2002, *Jiménez I. 1149* (LPB, UC); Prov. Carrasco, Sehuencas, encima cabañas del Country Club, 17°30'S, 65°17'W, 2250 m, 15 Dec 1993, *Ibisch 93-1894* (LPB), 3 km de Siberia hacia Karahuasi, 17°48'S, 64°41'W, 2400 m, 18 Oct 1996, *Kessler et al. 9141* (LPB, UC); Carretera Cochabamba-Villa Tunari, debajo de Corani, 17°10.51'S, 65°54.02'W, 2750 m, 26 Nov 2002, *Lehnert 519* (GOET, LPB, UC). **Santa Cruz**: Prov. Caballero, 7.5 km (by air) N of Comarapa, vicinity of Tinqué Laguna, 17°51'S, 64°32'W, 2625 m, 25 Nov 1999, *Nee 50639* (LPB, NY, UC).

Melpomene occidentalis* Lehnert, *sp. nov.* TYPE.—ECUADOR. **Zamora-Chinchipe**: New road Loja-Zamora, ca. 4 km E of pass “El Tiro,” ridge from white cross on left road side (towards the valley), 03°59'S, 79°08'W, 2550 m, 25 Sep 2004, *Lehnert 1343* (holotype: QCA; isotypes: GOET, UC). **Figs. 6, 7E.*

A *Melpomene firma* petiolis teretibus vel parce marginatis, glabris vel glabrescentibus (vs. valde marginatis adaxialiter pilosis), segmentis numquam deflexis (vs. basalibus deflexis), squamis latioribusque (0.8–1.6 vs. 0.4–0.6 mm) differt.

Plants predominantly epiphytic, rarely epilithic or terrestrial, growing in moss layers. *Rhizomes* moderately long to short, ascending to erect (Figs. 6A, B), (0.8–)1.2–1.8(–2.2) mm diam. *Fronds* to 22–28 cm long, erect (Figs. 6A, B), straight or weakly arching, inserted onto the rhizomes at acute angles, closely arranged (internodes 1–3(–5) mm), usually caespitose (Fig. 6B). *Scales* 6.0–9.0 × 0.8–1.6 mm, (18–)20–26 cells wide, clathrate, dark brown to brown, iridescent, bases cordate, tips long-acute to attenuate, margins with small hyaline retrorse papillae 1–3 cells long (Fig. 6C), apical cells 3–8, in a linear arrangement or nodding cluster (similar to Figs. 5C, H). *Petioles* (25–)30–95 (–140) mm long, 0.8–1.0 mm thick, terete (Fig. 6C) to weakly marginate throughout, without acicular or setiform/ciliform hairs, simple and branched clavate hairs of crosiers and young fronds sometimes persistent in older fronds. *Laminae* (110–)145–220(–330) × (22–)30–45(–80) mm, lanceate or

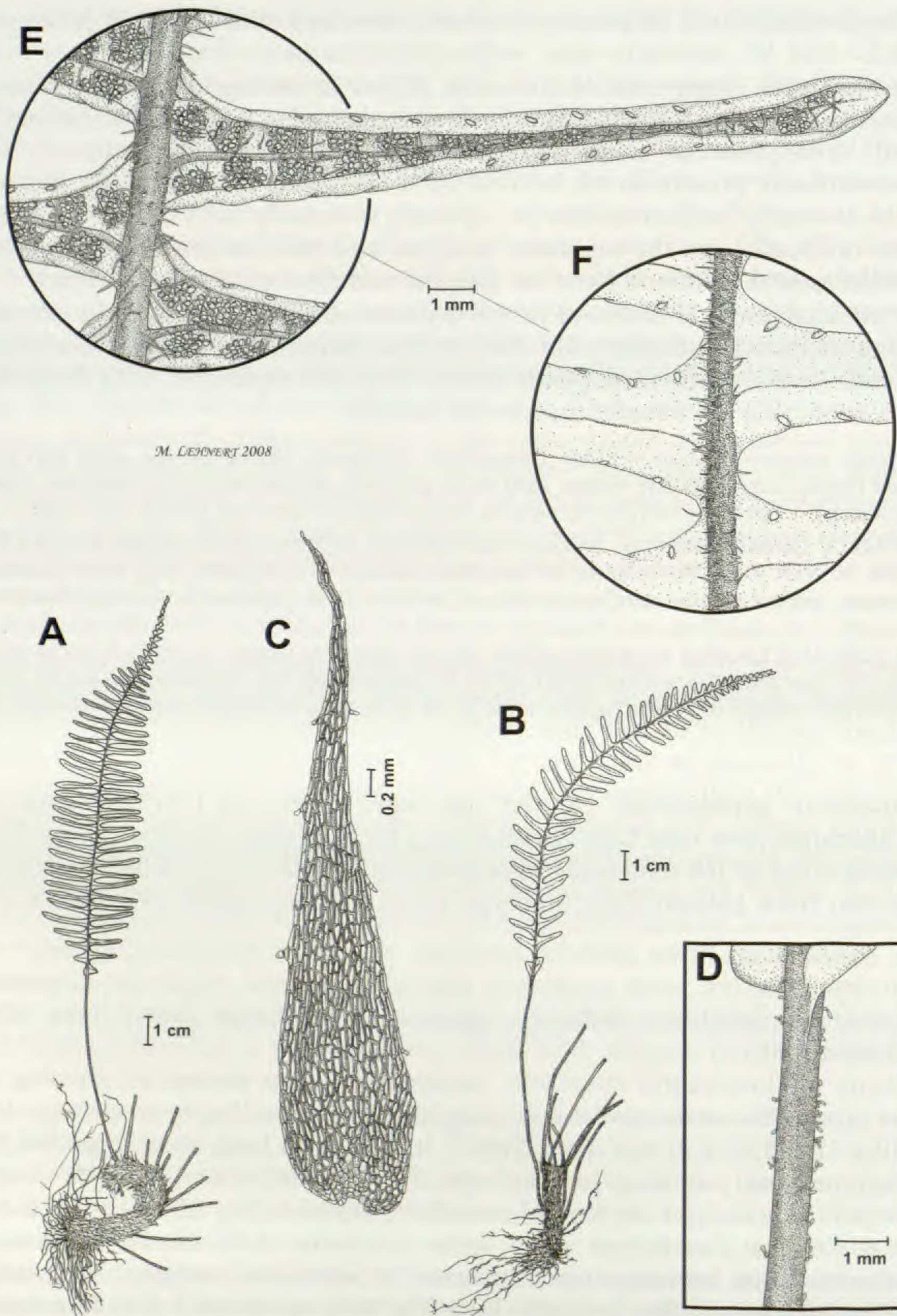


FIG. 6. *Melpomene occidentalis*. A. habit of plant with patent linear segments; B. habit of plant with ascending long deltate segments; C. scale; D. petiole, upper part; E. fertile segment abaxially; F. rachis adaxially (all from *Lehnert 1343, GOET*, except for B, *Lehnert 1575, GOET*).

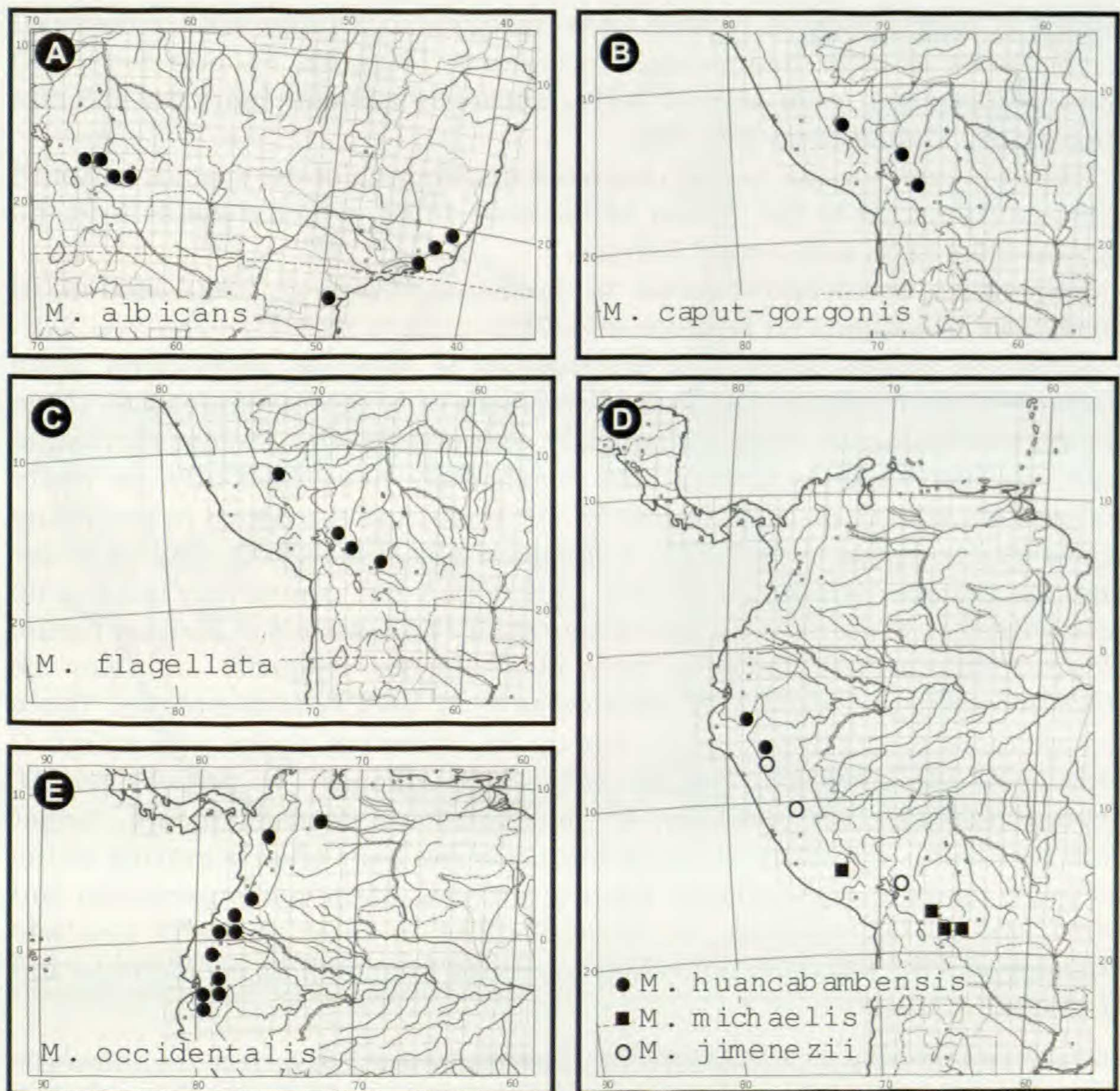


FIG. 7. Distribution of the new species. A. *Melpomene albicans*. B. *Melpomene caput-gorgonis*. C. *Melpomene flagellata*. D. *Melpomene huancabambensis* (dots), *M. jimenezii* (circles), and *M. michaelis* (squares). E. *Melpomene occidentalis*.

broadly elliptic (broadest in the middle), acute to attenuate at tip; bases rounded to cuneate (Figs. 6A, B). *Rachises* dark brown to black, planar to weakly protruding adaxially, hemispherically protruding abaxially, with few to many short, brown, acicular hairs to 0.2–0.8 mm long on both sides, usually adaxially hairier than abaxially (Figs. 6D, E). *Segments* (8–)16–20(–42) \times (1.5–)1.8–2.2(–4.4) mm (5–8 times longer than wide) (Fig. 6D), patent or weakly ascending (90° – 75°) (Figs. 6A, B), fully adnate, inequilateral at bases, weakly surcurrent towards the blade apices (Figs. 6D, E), linear to long-deltate, tips obtuse; margins entire (Fig. 6E) or dentate proximally in large segments; midveins visible on both sides of the segments (Figs. 6E, F); proximal segments pairs smaller than the central segments, but not auriculiform, not remote, or if remote then connected by a thin strand of laminar tissue; stomata sometimes

visible as dark brown to reddish dots; margins sometimes with ephemeral clavate hairs or cells; hydathodes conspicuous (Figs. 6E, F). *Sori* 5–12(–15) pairs per segment, with several stiff, castaneous acicular hairs 0.4–0.8 mm long mostly around them (Fig. 6E).

The name refers to the western centered distribution of the species in South America compared to the similar *Melpomene firma*, which extends E to the Guyana Highlands and central Bolivia.

Melpomene occidentalis grows in montane forests at 2100–3400 m in Venezuela, Colombia and Ecuador (Fig. 7E).

Molecular studies show that this species is sister to *Melpomene firma* (Lehnert *et al.*, in press). The main differences of *M. occidentalis* to *M. firma* are the predominantly terete, completely glabrous petioles (except for clavate hairs vs. petioles always marginate, persistently hairy adaxially, or rarely glabrescent, with dark, acicular hairs in *M. firma*) and the patent to ascending segments (vs. patent to deflexed). Colombian plants may have sinuses wider than the segment width (*Hagemann 1306*, COL), but contrary to the remote segments of *M. firma* they are still connected by thin strands of laminar tissue. Plants from northern Ecuador have more deltate segments and may be confused with species of the *M. pilosissima* or *M. personata* complexes. Those species differ in lacking marginal cells on the scales (vs. scales with marginal cells in *M. occidentalis*). The *M. pilosissima* alliance (*M. pilosissima*, *M. huancabambensis*, *M. jimenezii*, *M. michaelis*) has more abundant, longer hairs (to 3 mm), especially on the petioles, and has hairs often occurring on the segments margins or the adaxial laminar surfaces. *Melpomene personata* and allied species (*M. albicans*, *M. youngii*) differ in their generally prostrate rhizomes and the adaxially not visible midveins from both *M. occidentalis* and *M. firma*.

ADDITIONAL SPECIMENS EXAMINED.—VENEZUELA. **Tachirá:** Páramo Tarmá, near the Colombian-Venezuelan border, 2475–2550 m, 20–23 May 1967, *Steyermark et al. 98600* (NY). **Prov. unknown:** [Mérida?] Manzanos, 2800 m, *Lindig 300* (B, P).

COLOMBIA. **Antioquia:** San José de la Montaña, Alto El Cristo, 06°46'53"N, 75°41'45"W, 3420 m, 23 Jul 2002, *Rodriguez W. et al. 3513* (COL). **Huila:** Cordillera Central, Cordillera del Buey, hike from Finca Loyola over the páramo down to San Antonio, 2100 m, 14 Dec 1975, *Bishop 1993* (UC). **Nariño:** La Botana (Pasto region), 2900 m, 29 Oct 1972, *Hagemann & Leist 1306* (COL).

ECUADOR. **Cotopaxi:** Quevedo-Latacunga road, above Pilaló, 00°58'S, 78°58'W, 2850 m, 08 Apr 1973, *Holm-Nielsen et al. 3251* (UC); along Quevedo-Latacunga road, between Pilaló and Pujili, 00°59'S, 78°58'W, 3400 m, 26 Nov 2004, *Lehnert 1575* (GOET, QCA, UC). **Loja:** E of Nudo de Cajanuma, just N of "Centro de Información," sample plot site, 04°05'S, 79°10'W, 2900 m, 20 Sep 1989, *Bøgh 47959* (AAU); Parque Nacional Podocarpus, above Nudo de Cajanuma around "Centro de Información," 04°05'S, 79°10'W, 2800–3000 m, 16 Nov 1989, *Bøgh 86609* (AAU); Cerro Toledo, E of Yangana, between Loja and Valladolid, 04°23'S, 79°07'W, 3000–3100 m, 26 Oct 2004, *Lehnert 1464a* (GOET, QCA, UC); Cajanuma, SE of Loja, 04°07'S, 79°10'W, 2750 m, 03 Nov 2004, *Lehnert 1507* (GOET, QCA, UC). **Loja/Zamora-Chinchipe:** limit of Parque Nacional Podocarpus, around pass on road Loja-Zamora, 03°58'S, 79°07'W, 2900 m, 08 Jan 1989, *Madsen 85474* (AAU). **Morona-Santiago:** E of pass on Gualaceo-Limon road, 03°00.27'S, 78°39.10'W, 3000–3200 m, 16 Nov 2004, *Lehnert 1558a* (GOET, QCA, UC). **Napo:** Cartagena, km 25 from El Carmelo on road towards La Bonita, 00°37'N, 77°30'W, 2800 m, 13 Apr 1979, *Løjtnant et al. 12334* (AAU); outskirts of Pifo, 2500 m, 08 May 1935, *Mexia 7353a* (UC). **Pichincha:** carretera Quito-Santo Domingo, 2500 m, 24

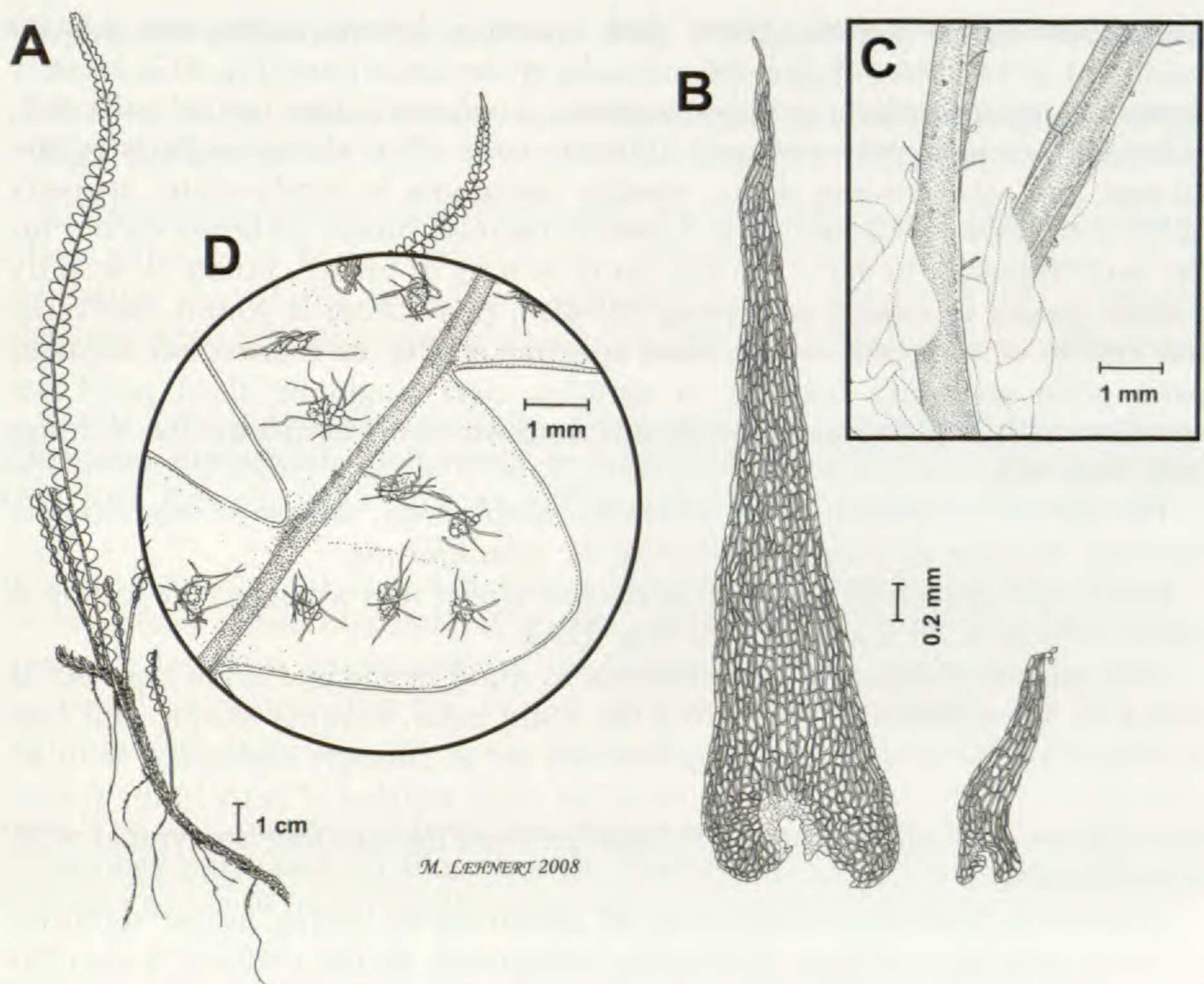


FIG. 8. *Melpomene paradoxa*. A. habit; B. scales, C. petioles; D. fertile segments abaxially, sporangia primordial (all from Kessler 6663, UC).

May 1987, *van der Werff & Palacios* 9600 (MO, UC). **Zamora-Chinchipe:** Estación Científica San Francisco, above refuge, along trail "Antennenbergweg," just below junction with trail T1, study plot A 5, 03°59'36.4"S, 79°04'03.2"W, 2660 m, 26 Sep 2003, *Lehnert* 909a (GOET, QCA, UC); new road Loja-Zamora, ca. 4 km E of pass "El Tiro," 03°59'S, 79°08'W, 2650 m, 23 Sep 2004, *Lehnert* 1332 (GOET, QCA, UC).

***Melpomene paradoxa* Lehnert, *sp. nov.* TYPE.** — BOLIVIA. **La Paz:** Prov. Nor Yungas, trocha al Valle Coscapa, Parque Nacional Cotapata, 16°12'S, 67°53'W, 3450 m, 09 Sep 1997, *Kessler et al.* 11717 (holotype: LPB; isotypes: GOET, UC). **Figs. 8, 12A.**

A *Melpomene moniliformi* squamis maioribus (squamis usque 2.0–2.5 mm longis cum 14–18(–20) cellulas supra basin vs. usque 3.5–4.0(–8.0) mm longis cum (20–)22–28(–32) cellulas), a *M. flabelliformi* absentia pilorum inter soros (vs. pilis inter soros dispersis) segmentisque brevioribus (rotundis, usque 4.5 mm longis vs. oblongis, usque 11.5 mm longis) differt.

Plants large, epiphytic in moss cushions. *Rhizomes* horizontal, long-creeping (Fig. 8E), (0.6–)0.8–1.2 mm diam. *Fronds* to 27–32 cm long, diffusely arranged (internodes 5–10 mm), not caespitose, mostly arching (Fig. 8E).

Scales lanceate to ovate-lanceate, dark brown to brown, iridescent, 3.5–4.0 (–8.0) \times 1.0–1.6 mm. (14–)22–28(–32) cells wide across base (Fig. 8C), broadly cordate to pseudopeltate at bases, acute to attenuate at tips; apical cells 3–8, bifurcately to palmately arranged, ultimate cells often elongate. *Petioles* 20–60 mm long, 0.5–0.8 mm diam., weakly marginate to rarely alate, sparsely hairy with hairs to 1.2 mm long. *Laminae* narrow, linear, glabrous except for the sori. *Segments* to 4.5 \times 4.0 mm (only as long as broad), lunate to broadly deltate, patent to weakly ascending (90–80°), tips obtuse to round, midveins not visible or obscurely so in dried specimens (Fig. 8F); proximal segment pairs often gradually reduced to auricles. *Sori* single or 2(–3) pairs per segment, with 5–10 brown to castaneous, setiform or ciliform hairs 0.8–1.2 mm long (Fig. 8F).

The species is named for its puzzling morphology, which is intermediate between *Melpomene flabelliformis* and *M. moniliformis*.

Melpomene paradoxa is known from elfin forests and wet montane forests at 2800–3700 m in Peru and Bolivia (Fig. 12A).

This species matches *M. flabelliformis* in the rhizome and scale size, but is closer to *M. moniliformis* regarding the scale color, laminar shape, and hair distribution. The scales of *M. paradoxa* are not as strongly iridescent as in *M. flabelliformis*, and despite having often the same amount of hairs in the sori as that species, *M. paradoxa* lacks the hairs between the sori that are typical of *M. flabelliformis*.

Melpomene flagellata differs from *M. paradoxa* in having longer setiform/ciliform hairs (1.2–1.8 mm) in a denser pubescence on the petioles; it also has most of the segment tips truncate (vs. always obtuse or rounded in *M. paradoxa*).

Melpomene caput-gorgonis has shorter petioles than *M. paradoxa*, often relatively wider, elliptic laminae (vs. laminae linear in *M. paradoxa*), and conspicuously multiple capitate hairs at the scale tips (vs. cells as a single branched clavate hair).

ADDITIONAL SPECIMENS EXAMINED.—PERU. **Ayacucho:** Condorcunca, 12 Oct 1964, *Barrón s.n.* (USM). **Cuzco:** Prov. Urubamba, between San Luis and Abra Málaga, Km 154, 13°05.4'S, 72°22.2'W, 3300 m, 16 Oct 2002, *Lehnert 439* (GOET, UC, USM); Machu Picchu, 4 km from the Runucuray-Sayacmarca pass in the Inca trail, above the lake between Sayacmarca and the pass (vegetation plot 166), 3665 m, 23 Aug 1982, *Peyton & Tilney Peyton 1570* (UC).

BOLIVIA. Cochabamba: Prov. Carrasco, Colomi, along road, 62.2 km from Cochabamba (Río Rocha), 17°12'84"S, 65°53'21"W, 3100 m, 30 Dec 1998, *de Boer 1156* (LPB); 108 km antigua carretera Cochabamba-Villa Tunari, 17°09'S, 65°38'W, 2950 m, 22 Jun 1996, *Kessler 6569* (LPB, UC); 94 km on old road Cochabamba-Villa Tunari, 17°12'S, 65°41'W, 3500 m, 28 Jun 1996, *Kessler et al. 6773* (GOET, LPB); road Cochabamba-Villa Tunari, below Corani, near Km 71+00, trail up the mountain, 17°10.59'S, 65°53.67'W, 2800 m, 27 Nov 2002, *Lehnert 525* (LPB). **La Paz:** Prov. Bautista Saavedra, Charazani, E of Chullina, 3500 m, 22 Dec 1993, *Herzog H87* (LPB); Prov. Nor Yungas, Unduavi, 3300 m, Nov 1910, *Buchtien 70* (P); roadside bank between Cotapata and Chuspipata, S-facing, La Paz-Caranavi road, 16°17'S, 67°50'W, 3200 m, 15 Aug 1990, *Fay & Fay 3034* (LPB, MO); trench to the Valle Coscapa, Parque Nacional Cotapata, 16°12'S, 67°53'W, 3450 m, 09 Sep 1997, *Kessler et al. 11717* (LPB, UC); Unduavi, trench to the Valle de Coscapa, 3400 m, 17 Dec 2002, *Lehnert 536, 539, 542* (GOET, LPB, UC); 1 km W of Chuspipata, 16°17'S, 67°49'W, 3140 m, 24 Mar 1982, *Solomon 7260* (LPB, UC).

Melpomene personata Lehnert, *sp. nov.* TYPE.—BOLIVIA. **La Paz:** Prov. Bautista Saavedra, 15 km de Charazani hacia Chullina, 15°10'S, 68°53'W, 3400 m, 05 Jul 1996, Kessler 10606 (holotype: UC; isotypes: GOET, LPB). **Figs. 9, 12B.**

A *Melpomene pilosissima* rhizomatibus longioribus horizontaliter reptantibus pilisque in soris confertis (vs. rhizomatibus brevibus erectis, pilis aequaliter distributis in pagina abaxiali), a *M. youngii* et *M. albicante* absentia strati albi in pagina abaxiali (vs. pagina abaxiali alba vel albicante) differt.

Plants predominantly epiphytic, rarely epilithic, growing in moss layers. *Rhizomes* horizontal, moderately to long-creeping, 0.8–1.2(–1.5) mm diam. (Fig. 9A). *Fronds* 14–33 cm long, stiffly pendent, inserted onto the rhizome at right angles, diffusely arranged (internodes 3–10 mm), not caespitose (Fig. 9A). *Scales* (2.0–)3.0–4.5(–6.0) × (0.3–)0.4–1.0 mm, (8–)10–14(–22) cells wide across base, clathrate (Fig. 9B), dark brown to brown, iridescent, narrowly lanceate, bases cordate, tips long-acute to attenuate; apical cells 1–3, linearly arranged (Fig. 9B) or 2–5 cells palmately arranged. *Petioles* 20–150 mm long, 0.6(–0.8) mm thick, terete or weakly marginate from the lowest segments, with few to many dark brown setiform/ciliform hairs 0.9–2.0 mm long (Fig. 9C); simple and branched clavate hairs of crosiers and young fronds sometimes persistent on older fronds. *Laminae* to 155–180(–220) × 26(–40) mm (2/3 to 3/4 of frond length, rarely less in single fronds of a plant), broadly linear to narrowly elliptic (broadest in the middle), bases cuneate to short-tapering, apices long-acute (Fig. 9A). *Rachises* dark brown to black, planar and slightly sunken between the segments adaxially (Fig. 9E), hemispherically protruding abaxially (Figs. 25D, F), sparsely hairy on both sides (Fig. 9E), usually more hairs abaxially, setiform/ciliform hairs to 1.2 mm long, brown. *Segments* 8.0–15.0(–22.0) × 1.2–2.5(–3.5) mm (6–8 times long than broad), ascending (70–60°), equilateral at base or weakly decurrent towards the bases, fully adnate, linear-oblong, the tips acute to obtuse (Fig. 9A); midveins visible abaxially (e.g. Jiménez I. 1773; Fig. 9D), at least discontinuously so (Fig. 9F); proximal 2–6 segment pairs markedly smaller than the subsequent segments (Fig. 9A), lowest ones usually auriculiform; setiform/ciliform hairs few (Fig. 9F) to many on the midveins, absent on margins and adaxial laminar surfaces; hydathodes present (Fig. 9E). *Sori* 2–10 pairs per segment, with 6–10 setiform or ciliform hairs 0.8–1.0 mm long (Fig. 9F).

The name alludes to the fact that the species has often been mistaken for *M. pilosissima* (Latin, *personata* = masked, disguised), and also alludes to the name of the genus: Greek actors wore masks (Latin, *persona*) to symbolize the different characters of the plays, including the tragedies that the muse Melpomene is representing.

Melpomene personata grows in shrubby páramos, elfin forests, and wet montane forests at (1850–)2700–4500 m in Mexico, Guatemala, Costa Rica, Panama, Dominican Republic, Venezuela, Colombia, Ecuador, Peru, and Bolivia (Fig. 12B) and is a common species in the Andes.

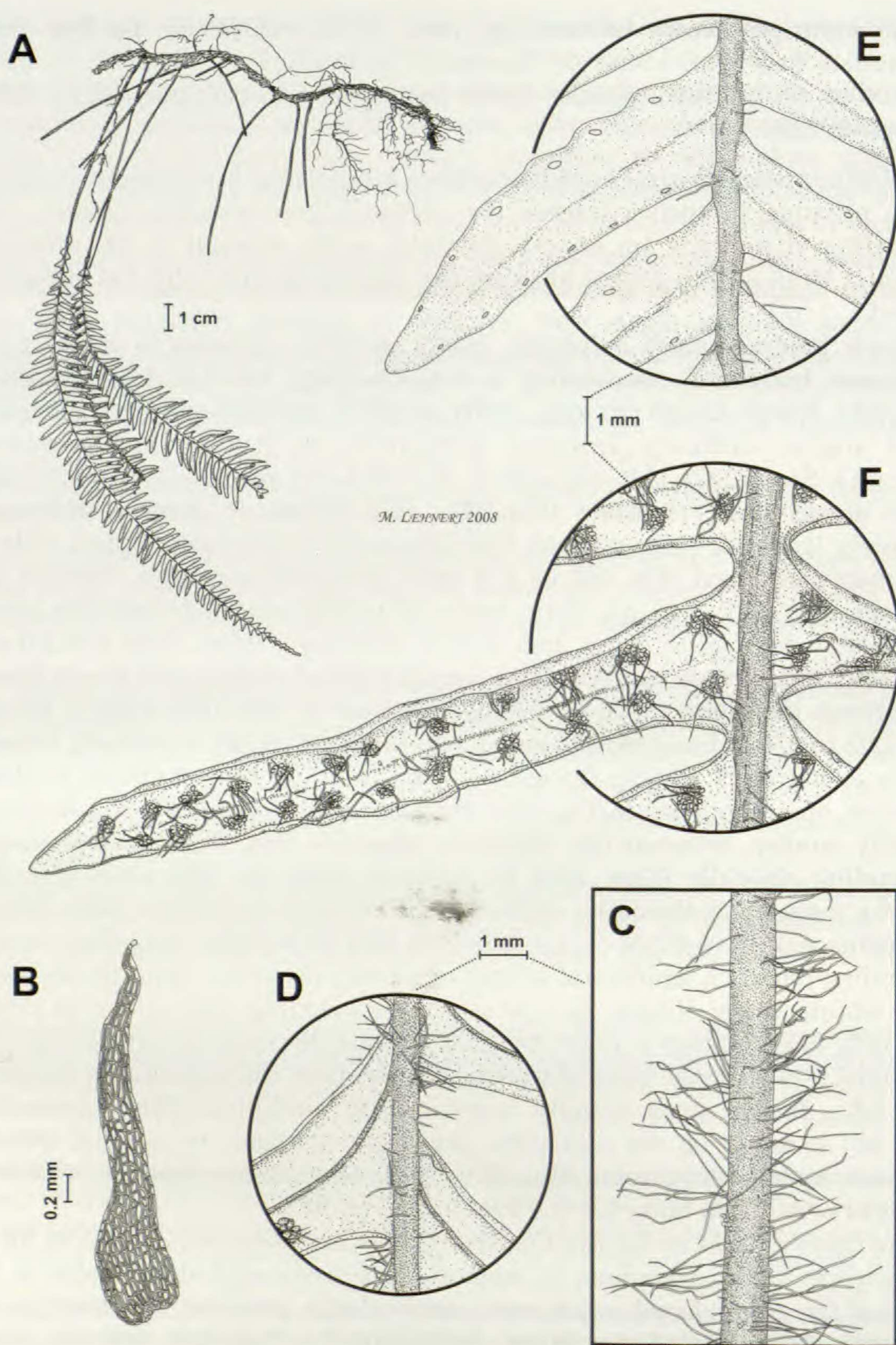


FIG. 9. *Melpomene personata*. A. habit (Lehnert 405, GOET); B. scale (Lehnert 145, GOET); C. petiole (Bach et al. 1080, GOET); D. rachis and segments abaxially, midveins clearly visible (Jiménez I. 1773, UC); E. segment adaxially, margins undulate (Kessler et al 7234, GOET); F. fertile segment abaxially, sporangia primordial, midveins obscurely visible (Bach et al. 1080, UC).

Many Central American plants differ from the Andean ones slightly in having more but smaller, isodiametric cells in the scales, more apical cells, and mostly weakly visible midveins. Apart from that, the characters are identical. Many specimens of *M. personata* have been erroneously determined as *M. pilosissima*, which has added greatly to the confusion within that species complex. Molecular data, however, indicate that *M. personata* is not closely related to *M. pilosissima* and allies, but in fact belongs to the *M. moniliformis* clade (Lehnert *et al.*, in press). Morphologically, *M. personata* is characterized by horizontally creeping rhizomes (vs. usually erect in *M. pilosissima*); rhizome length can vary greatly, but usually is longer than in *M. pilosissima* and allies, with the fronds also placed further apart (3–10 mm vs. 0.5–2.0 mm in *M. pilosissima*). From *M. pilosissima* and *M. huancabambensis*, *M. personata* differs in having the hairs abaxially clustered in the sori and along the midveins (vs. hairs evenly distributed); from *M. xiphopteroides*, it differs in the terete petioles (vs. petioles marginate to alate); from *M. huancabambensis*, *M. jimenezii*, and *M. michaelis* in having shorter hairs (to 2 mm in *M. personata* vs. to 3 mm) and conspicuous hydathodes (vs. hydathodes reduced or lacking); from *M. vernicosa* and *M. jimenezii* in the thinner (0.4–0.8 mm vs. 0.8–1.5 mm), glabrous or glabrescent petioles (vs. petioles persistently hairy).

Other species for which *Melpomene personata* may be mistaken include *M. sodiroi*, *M. albicans*, and *M. youngii*. All differ from *M. personata* in having hidden midveins on the abaxial laminae (vs. midveins at least obscurely visible in *M. personata*). *Melpomene sodiroi* also has larger scales and usually gibbose segments; *Melpomene albicans* and *M. youngii* have a white wax-like deposit on the abaxial laminae, which is not present in *M. personata*; furthermore, *M. youngii* is completely glabrous and generally lacks hairs in the sori (sometimes 1–2 hairs in sori vs. hairy petioles, hairs clustered in sori in *M. personata*).

The Peruvian collection *Philippi s.n.* (B) belongs to *Melpomene personata* and was annotated as paralectotype of *Polypodium firmum* Klotzsch (= *Melpomene firma*). These two species can be easily distinguished, as *M. firma* (including the lectotype *Schomburgk 1170*, B) has an erect rhizome, patent segments, truncate laminar bases and small cells along the scale margins, while *M. personata* (including *Philippi s.n.*, B) has horizontally creeping rhizomes, ascending segments, rounded to cuneate laminar bases, and lacks marginal cells on the scales.

ADDITIONAL SPECIMENS EXAMINED.—MEXICO. **Chiapas:** San Cristobal Las Casas, E side of Zontehuitz near summit, 2800 m, 30 Nov 1971, *Breedlove 22928* (NY); Union Juárez, SE side of the summit of Volcán Tacaná, 3600 m, 03 Mar 1972, *Breedlove 24310* (NY); *ibid.*, 10 Nov 1972, *Breedlove 29353* (NY); Mount Tacana, 2000–4038 m, Aug 38, *Matuda 2379A* (NY); N of San Cristobal las Casas on top of Cerro Zontehuitz, 3100 m, 27 Jul 1963, *Mickel 1247B* (NY).

GUATEMALA. **Chimaltenango:** Cerro de Tecpám, region of Santa Elena, 2400–2700 m, 26 Dec 1938, *Standley 61075* (NY). **Guatemala:** Hyw. No. 1, 2900 m, 21 Feb 1947, *Brenckle 47–61* (UC). **Huehuetenango:** Limestone region 3–15 km N of Chemal, Sierra de los Cuchumatanes, 3400 m, 02 Dec 1962, *Molina-R. et al. 22138* (NY); Sierra Cuchumatanes between Km 136 to 150 to San Juan Ixcay, 3000–3500 m, 12–23 Jan 1966, *Molina-R. et al. 16541* (NY). **Totonicapán:** Maria Tecún, 3000–3600 m, 12–23 Jan 1966, *Molina-R. et al. 16357* (NY).

COSTA RICA. Cartago: Cerro de la Muerte, 1 km NW of Villa Mills on Interamerican Highway, behind Hotel La Georgina, 2900 m, 08 Aug 1967, *Mickel 3203* (NY); Km 89 Rt. 2 to páramo de la Muerte and San Isidro, 09°35'N, 83°42'W, 3300 m, 30 Oct 1993, *Rivero 2488, 2494, 2495, 2497* (UC); Cantón de Paraíso, R.F. Río Macho, cuenca del Reventazón, carretera interamericana, road Cartago-San Isidro, cerro de la Muerte, 3150–3300 m, 09°34'30"N, 83°45'W, 21 Apr 1999, *Rojas A. 5082* (NY). **San José:** Cerro de la Muerte; 1 km NW of Villa Mills on the Interamerican Highway, cross from Hotel La Georgina, 2900 m, 08 Aug 1967, *Bishop 869* (UC); along Inter-American Highway, Cerro de la Muerte, 09°35'N, 83°45'W, 3220 m, 18 Nov 1986, *Hennipman et al. 7010* (UC); Cerro Sákira-páramo, 3300 m, Feb 2003, *Kluge 1182* (GOET); Massiv of Cerro de La Muerte, 3200 m, 15 Jul 2003, *Kluge 6841* (GOET); *ibid.*, 3300 m, 16 Jul 2003, *Kluge 6909, 6910* (GOET); *ibid.*, 3400 m, 17 Jul 2003, *Kluge 6946* (GOET); road from Cartago to San Isidro del General (Pan American Highway, Rt. 2), Km 96–97, ca. 1.5 km S of Villa Mills (near Siberia), 2900 m, 29 Jan 1986, *Smith A. R. & Béliz 2061* (UC).

PANAMA. Chiriqui: between Itamut and Bine Peaks, Fabrega massif, Bocas del Toro, 3200 m, 05–09 Mar 1984, *Gómez L. D. et al. 22539* (UC); Volcán Baru, on road to towers at top, near towers at summit, 08°47'N, 82°32'W, 3300–3400 m, 13 May 1990, *McPherson 15054* (UC).

DOMINICAN REPUBLIC. Peravia: 48 km S of Constanza (on road to San José de Ocoa), in area of La Nevera, 18°41'N, 70°35.5'W, 2070 m, 4 Mar 1981, *Zanoni & Mejia 12209A* (NY).

COLOMBIA. Antioquia: Guatapé, Vereda Santa Rita, finca Montepinae, 1850 m, 06°15'N, 75°10'W, 06 Mar 1990, *Contreras & Echeverri 217* (NY). **Boyacá:** Sierra Nevada de Cocuy, on steep S side of the Valle del Corallitos, at lower edge of this near river, 4000 m, 06 Sep 1957, *Grubb & Guymer P102* (AAU); between Arcabuco and Villa de Leyva, trail Las Coloradas, above El Charizal, 3420 m, 31 Aug 1967, *Jaramillo Mejia et al. 3166* (AAU). **Cauca:** Cordillera Central, Parque Nacional de Puracé, trail from Pilimbalá to the volcano of Purace, 3700 m, 10 Jul 1976, *Jaramillo Mejia & van der Hammen 5219* (AAU). **Cundinamarca:** Laguna de Chisacá and surroundings, 3900–4200 m, 19 Oct 1958, *Bishler 1517* (COL); Fómeque, Parque Nacional Natural Chingaza, surroundings of laguna de Chingaza, E shore of Río Chuza, 2990 m, 05 Oct 1981, *Franco P. et al. 495* (AAU); Cogua, Vereda Quebrada Hóna, Reserva Forestal Protectora, 3200–3300 m, Aug–Oct 2003, *Trujillo 13* (COL). **Santander:** Coromoro, laguna La Fiquera, quebrada de Coromoro, 3750 m, 29 Nov 1967, *Jaramillo Mejia & van der Hammen 4380* (AAU); road between Bucaramanga and Pamplona, W slope of Páramo de Berlin, El Picacho, 3300 m, 11 Nov 1969, *Murillo M. T. & Jaramillo Mejia 1342* (AAU). **Prov. unknown:** Excursion to the Llanos de San Martin, Toquiza area, *Stübel 704* (B).

VENEZUELA. Mérida: Dtto. Justo Briceño, Páramo Piedras Blancas, Laguna La Fea, SE de la Carretera Vía Piñago, 3950–4500 m, 09 Jul 1982, *Briceño et al. 635* (AAU); Dtto. Libertador, Parque Nacional Simón Bolívar, camino del teleférico (de la Aguada), Laguna La Fría, vertiente septentrional de la Sierra Nevada de Mérida, 2700–3000 m, 21 Dec 1984, *Pipoly et al. 6542* (UC); Dtto. Rangel, Las Escaleras-Laguna El Boquerón, páramo de Minugú, unos 10 km al SE de San Rafael de Mucuchíes, 3150–3400 m, 21 May 1972, *Ruiz-Teran 7314* (UC). **Trujillo:** Dtto. Carache, via Páramo Cendé sitio denominado “Las Cruces,” 09°33'N, 70°08'W, 27 Nov 1987, *Rivero & Diaz W. 1495* (UC).

ECUADOR. Azuay: Recreation Park Cajas, 4000–4100 m, 02 Sep 1984, *Jaramillo J. 7198* (AAU); Cajas, N of Laguna Toreadora, 02°47.17'S, 79°13.10'W, 3850 m, 17 Nov 2003, *Lehnert 1116* (GOET, QCA, UC). **Carchi:** Montufar, within 3 km of pueblo of Colonia Huaqueña, 00°35.5'N, 77°42'W, 3500 m, 30 Jun 1994, *Fay & Fay 4342* (AAU); base of Volcán Chiles, km 34–36 on road Tulcán-Maldonado, 3900–4050 m, 00°47'N, 77°57'W, 19 May 1973, *Holm-Nielsen et al. 5922* (AAU, UC); El Angel-Tulcán main road, Km 1, turnoff towards W, ca. 8 km, 00°34'N, 77°54'W, 3460 m, 08 Aug 1990, *Jørgensen et al. 92264* (AAU); road Tulcán-Maldondado, Km 32 de Tulcán, base del Volcan Chiles, *Lehnert 145, 146* (GOET, QCA, UC). **Chimborazo/Cañar:** W escarpment between Santa Rosa and Joyagshi, 2500–2700 m, 06–09 Jul 1945, *Camp 4076* (NY). **Imbabura:** Laguna Grande de Mojanda, 15 km S of Otavalo, 3750 m, 00°08'N, 78°16'W, 14 May 1985, *Eriksen 59365* (AAU); road Ibarra-Mariano Acosta, E of the pass, 00°20'N, 78°00'W, 3500–3600 m, 09 Aug 1976, *Øllgaard & Balslev 8585, 8579* (AAU).

PERU. **Cuzco:** Prov. Paucartambo, Pillahuata, near Tres Cruces, + 130 km from Cuzco to Pilcopata, 13°05'S, 71°30'W, 2000 m, 13 Dec 1986, *Núñez 7798* (CUZ, LPB); Achirani, Marcachea, 3000 m, 30 Jul 1939, *Vargas C. 1573* (CUZ); Dtto. Marcachea; near Achirani, 2600 m, 30 Jul 1939, *Vargas C. 11141* (CUZ, UC); Prov. Urubamba, Abra Málaga, 4330 m, 16 Oct 2002, *Lehnert 423* (GOET, UC, USM); Machupicchu, at 88 km and 112 km from Cuzco, Santuario Histórico de Machu Picchu and along Inca trail, in Qorihuayrachina, llulluchayoc, Ronkuraky, Phuqupatamarca, Wiñayhuayna, and Intipunco, 13°09'10"S, 72°31'W, 4150 m, 14–22 Oct 1987, *Núñez & Arque 8339* (UC); Altura Colca, Valle de Lares, 9000 ft, Mar 1932, *Bües 1807* (CUZ). **Junin:** Prov. Satipo/La Convención, Cordillera Vilcabamba, Río Ene slope, near summit of divide, 3350–3400 m, 11°39'36"S, 73°40'02"W, *Boyle et al. 4326* (UC, USM); Prov. Tarma, high region of second Cordillera, valley of Marañoch near Tarma, 1840, *Philippi s.n.* (B, isosyntype of *Polypodium firmum* Klotzsch). **San Martin:** Mariscal Cáceres, Chochos, NW corner of Río Abiseo National Park, 3500 m, 15 Jul 1987, *Young & León 4716* (USM).

BOLIVIA. **Cochabamba:** Prov. Ayopaya, 2 km al SE de Saila Pata, 16°55'S, 66°55'W, 3550 m, 15 Nov 1997, *Kessler et al. 12475* (GOET, LPB, UC); Prov. Carrasco, 100 km [on] old road Cochabamba-Villa Tunari, 17°12'S, 65°42'W, 3250 m, 26 Jun 1996, *Kessler 6728* (GOET, LPB, UC); *ibid.*, 115 km, 17°07'S, 65°38'W, 2700 m, 01 Jul 1996, *Kessler et al. 6862* (GOET, LPB, UC); *ibid.*, 63 km, 17°15'S, 65°43'W, 3750 m, 02 Jun 1996, *Kessler et al. 6887* (GOET, LPB); *ibid.*, 68 km, 17°14'S, 65°13'W, 3600 m, 11 Jul 1996, *Kessler et al. 7234* (GOET, LPB, UC); Prov. Chapare, ca. 8 km N [of] Maycamayu, ca. 70 km from Sacaba, 17°12'S, 65°57'W, 3350 m, 12 Aug 1991, *Kessler 2919* (AAU, LPB). **La Paz:** Prov. Franz Tamayo, PN-ANMI Madidi, trail Pelechuco-Mojos, locality Tambo Quemado (camping site), going down along the trail, a little past the second river, 14°41'S, 68°58'W, 3470 m, 29 Apr 2003, *Jiménez I. 1773* (GOET, LPB, UC); Prov. Inquisivi, some 8 km from Quime towards Inquisivi, Camillaya arriba del pueblo, 16°58'S, 67°12'W, 3000 m, 29 Dec 1997, *Beck 24364* (LPB); Prov. Murillo, arriba de la laguna de Viscachani al valle de Zongo, 16°13'S, 68°07'W, 4050 m, 10 Oct 1995, *Kessler et al. 5885* (AAU, LPB); Prov. Nor Yungas, Estación Biológica Tunquini, senda del Pantanón a Hornuni, 16°11'S, 67°53'W, 3350 m, 19 Sep 2000, *Bach et al. 1080* (GOET, LPB, UC); pasando Unduavi antes de llegar a Cotapata, subiendo la senda antigua hacia Coroico, 3500 m, 22 Oct 1994, *Beck & Ruthsatz 21492* (GOET, LPB, UC); Valle de Coscapa, 16°17'S, 67°51'W, 3400 m, 02 Oct 2002, *Lehnert 396, 398, 404, 405* (GOET, LPB, UC); *ibid.*, 17 Dec 2002, *Lehnert 535, 537, 538, 541* (GOET, LPB, UC); Prov. Sud Yungas, Unduavi, near the mine Lourdes, 16°18'S, 67°52'W, 3450 m, 25 Nov 1995, *Gonzales et al. 1557* (LPB, UC).

***Melpomene sklenarii* Lehnert, sp. nov.** TYPE.—ECUADOR. **Azuay:** Cajas National Park, E flanks of Cerro Amarillo (4451 m), 02°45'S, 79°15'W, 13 Jul 1997, 4300–4400 m, *Sklenar & Sklenarova 2592* (holotype: UC, isotype: PRC). **Figs. 10, 12C.**

A *Melpomene peruviana* squamis ovato-lanceolatis (vs. angusto-lanceolatis) frondibusque erectis distantibus (vs. frondibus pendentibus approximatis), a *M. moniliformi* et *M. flabelliformi* pilis aequaliter distributis in paginis abaxialibus (vs. pilis absentibus vel in soris restrictis) segmentisque basalibus interdum remotis (vs. segmentis semper confertis) differt.

Plants terrestrial or epilithic, growing in moss layers, rock crevices, or open soil. *Rhizomes* moderately to long-creeping, 0.6–1.0 mm diam. (Figs. 10A, B), regularly branching at wide to right angles (Fig. 10B). *Fronde*s to 13 cm long, erect, inserted onto the rhizomes at right angles, diffusely arranged (internodes (5–)11–14 mm), not caespitose (Fig. 10A, B). *Scales* 2.8–4.0 × 0.6 mm, (10–)14–18(–26) cells wide across their bases, clathrate (Fig. 10 C), dark brown to brown, weakly to rarely strongly iridescent, broadly cordate to pseudopeltate, acute to attenuate at tips; apical cells 3–8, palmately arranged; scales soon

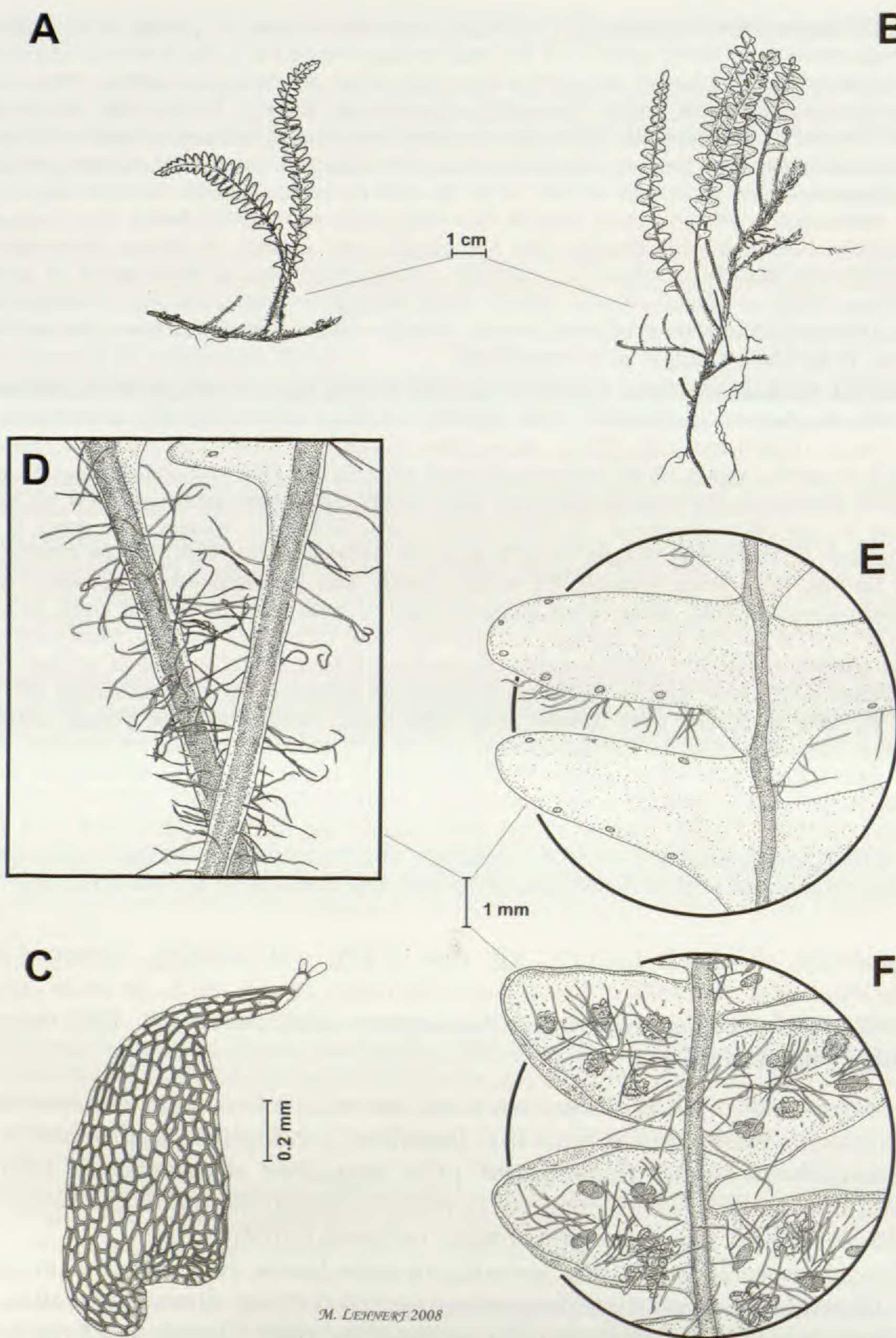


FIG. 10. *Melpomene sklenarii*. A. habit (Lehnert 156, GOET); B. habit (Lehnert 108, GOET); C. scale (Mille s.n., P); D. petioles (Lehnert 156, GOET); E. segments adaxially (Lehnert 156, GOET); F. segments abaxially, sporangia primordial to immature, partly removed (Lehnert 156, GOET).

shed from rhizomes, especially between the fronds. *Petioles* (6–)12–55 mm long, 0.4–0.8(–1.0) mm thick, alate from the laminar bases, marginate towards the rhizomes, glabrescent or hairy, with dark brown, ciliform/setiform hairs 0.75–1.5(–2.0) mm long (Fig. 10D); simple and branched clavate hairs rarely present; petiolar bases with persistent scales. *Laminae* 40–80(–90) mm long, to 7–12 mm wide, firm-chartaceous to subcoriaceous, linear to narrowly lanceate (widest below the middle), round to weakly cuneate at bases, acute at tips (Figs. 10A, B). *Rachises* dark brown to black, planar and slightly sunken between the segments adaxially (Fig. 10E), weakly protruding to planar abaxially, with scattered brown acicular or setiform/ciliform hairs to 1.2 mm long abaxially (Fig. 10F). *Segments* to $4.2 \times (2.0\text{--})2.4\text{--}3.0$ mm (ca. 1.5–2.5 times longer than broad), patent, inequilateral and decurrent towards the bases, fully adnate, deltate to oblong, the tips round to obtuse (Figs. 10E, F), slightly gibbose, abaxially pale green to whitish, but without wax-like deposit; midveins not visible, or obscurely so in dried specimens; basal pairs often remote, not notably smaller than the following segments, or only one pair weakly so (Fig. 10B); abaxially glabrous to densely hairy with evenly distributed, brown ciliform hairs 0.8–1.5 mm long (Fig. 10F); segment margins hyaline, one cell wide (2 cells wide in sinuses and at junctions with petioles), without clavate hairs (Fig. 10E, F); hydathodes present. *Sori* 1–3(–4) pairs per segment, surrounded by 5–8 dark brown setiform/ciliform hairs to 1.0 mm long (Fig. 10F).

The name honours Petr Sklenar from Charles University, Prague, who collected most of the known specimens during his studies of Ecuadorian páramos.

Melpomene sklenarii grows in páramos, punas (jalca), and elfin forests at 2900–4700 m in Colombia and Ecuador (Fig. 12C).

This species is easily confused with *M. peruviana* but can be distinguished by the evenly distributed hairs on the abaxial laminar surfaces (vs. clustered in sori in *M. peruviana*), more widely spaced fronds (internodes (5–)11–14 vs. 0.8–3.0 mm), and paler, more broadly lanceate rhizome scales (vs. dark brown to blackish and narrowly lanceate) which are often shed between the fronds (vs. usually persistent). *Melpomene sklenarii* grows in loose formations with the distant fronds held erect whereas *M. peruviana* tends to form dense mats and holds the fronds stiffly tip-downwards (or appressed to horizontal substrates).

The rather small range of *Melpomene sklenarii* matches that of *M. vulcanica* and both species apparently often grow closely together. Large specimens of *M. vulcanica* are easily separated (segments long-deltate with acute tips, midveins visible on both sides in *M. vulcanica* vs. segments oblong to deltate with round to obtuse tips, midveins not visible adaxially in *M. sklenarii*), but smaller plants may have these distinguishing characters more weakly developed and may be confused with *M. sklenarii*. Even if equal in size, *Melpomene vulcanica* has rhizome scales that are still larger (6.2×1.0 mm, 20–30 cells wide across bases vs. to 3.5×0.6 mm, 14–18(–26) cells wide across bases) and longer persisting than those of *M. sklenarii*. Both species have hyaline segment

margins, but those of *M. vulcanica* are two cell rows wide and beset with cells or clavate hairs whereas those of *M. sklenarii* are just one cell row wide in most parts and lack separate cells.

Small plants of *M. flabelliformis* can be distinguished from *M. sklenarii* by their setiform/ciliform hairs clustered in the sori and the proximally more strongly cuneate laminae with approximate segments (vs. hairs not clustered in sori and laminae proximally rounded to cuneate with often distant segments in *M. sklenarii*). The two species have not been found growing together so far, and especially the small forms of *M. flabelliformis* occur mainly outside the range of *M. sklenarii* (i.e., Mexico and Africa).

ADDITIONAL SPECIMENS EXAMINED.—COLOMBIA. **Nariño:** Prov. Pasto, Volcán Galeras, [ca. 01°12'N, ca. 77°28'W,] 3950 m, 06 Aug 1977, *Pinto et al. 1828* (COL). **Boyacá:** Cordillera Oriental, Sierra Nevada del Cocuy, surroundings of Salto de Correlitos, Sta. 13 above and E of Salto, E of Laguna San Paulito, ca. 05°34'N, ca. 72°37'W, 4200 m, 14 Apr 1959, *Barclay & Juajibioy 7370* (COL); Sierra Nevada del Cocuy, páramo Cocavo, Cuchilla Puente Piedra ca. 2 km to the NE of Laguna Pintada, 4510 m, 30 Sep 1972, *Cleef 5668* (COL). **Caldas:** Páramo del Ruiz, [ca. 05°28'N, ca. 75°39'W,] 4200–4630 m, 29 Aug 1957, *Barclay 5240* (COL); Nevado del Ruiz, [ca. 05°28'N, ca. 75°39'W,] 4700 m, 06 Aug 1958, *Bishler 1482* (COL); *ibid.*, sandy area 2 km SW of the refuge with many outcrops of volcanic rock, [ca. 05°28'N, ca. 75°39'W,] 4520 m, 18 Mar 1972, *Cleef & van't Hart 2446* (COL); road from Manizales to Nevado, above the “termales,” 3500 m, 07 Jun 1966, *Murillo M. T. et al. 861, 874* (COL); road from Manizales to Nevado, 4230 m, 05 Jul 1959, *Pinto 437* (COL); Cordillera Central, surroundings of the refuge of Ruiz, road to El Silencio, [ca. 05°28'N, ca. 75°39'W,] 4310 m, 07 Oct 1978, *Rangel et al. 1735-A* (COL).

ECUADOR. **Carchi:** road Tulcán-Maldonado, Km 32 from Tulcán, base of Volcan Chiles, 06 Jul 2002, *Lehnert 155a* (GOET, QCA, UC); road Tulcán-Maldonado, Km 34 from Tulcán, 06 Jul 2002, *Lehnert 156* (GOET, QCA, UC); S slopes of volcán Chiles, 02°49'N, 77°57'W, 4100 m, 21 Oct 1987, *Ramsay & Merrow-Smith 872* (AAU). **Chimborazo:** El Altar, N side of the volcano, on the ridge below the Canonigo peak, 01°41'S, 78°24'W, 4200–4400 m, 19 Aug 1995, *Sklenar & Kostecovarov 967* (UC); El Altar, N side of the volcano, on the ridge below the Canonigo peak, 01°41'S, 78°24'W, 4500 m, 19 Aug 1995, *Sklenar & Kostecovarov 88_7* (UC); Chimborazo volcano, base of the terminal moraine on the E side of the mountain, 01°28'S, 78°46'W, 4500 m, 03 Jul 1997, *Sklenar & Sklenarova 2198* (UC); Chimborazo volcano, on the E slope of the mountain, 01°28'S, 78°46'W, 4200–4250 m, 02 Jul 1997, *Sklenar & Sklenarova 2308* (UC). **Chimborazo/Morona-Santiago:** Cerro Yanaurcu, N ridge of the mountain, 02°14'S, 78°30'W, 4200–4300 m, 29 Oct 1995, *Sklenar & Kostecovarov 1499* (AAU); Cerros Yuibug-Pailacajas (4730 m), E side of the mountain ridge, 01°45'S, 78°27'W, 4300–4350 m, 31 Jul 1997, *Sklenar & Sklenarova 3025* (UC). **Imbabura:** SW slopes of the volcano Cotacachi, 00°22'N, 78°21'W, 4100–4320 m, 09 Nov 1983, *Boysen Larsen et al.* (AAU); slopes of Volcán Cotacachi, 00°35'N, 78°20'W, 4150 m, 11 Oct 1987, *Ramsay & Merrow-Smith 796* (AAU); Cerro Imbabura, in a gully on the S side of the volcano, 00°15'N, 78°10'W, 4400 m, 05 Jun 1995, *Sklenar & Kostecovarov 520* (AAU); Nevado Cotacachi, SE ridge of the volcano, 00°21'N, 78°21'W, 4200–4400 m, 09 Sep 1995, *Sklenar & Kostecovarov 1237* (UC); Cerro Imbabura, 00°15'S, 78°10'W, 4300 m, 05 Jun 1995, *Sklenar & Kostecovarov 31–16* (QCA), 31–17 (AAU). **Loja:** Cerro Toledo, E of Yangana, between Loja and Valladolid, 04°23'S, 79°07'W, 3000–3100 m, 26 Oct 2004, *Lehnert 1465* (GOET, QCA, UC). **Napo:** Laguna Yuragcocha, 3 km E of Cerro Quilindaña, 00°47'S, 78°21'W, 4050 m, 31 Mar 1979, *Holm-Nielsen 16375* (AAU); the SW slope 1.5 km from Cerro Quilindaña, 00°47'S, 78°21'W, 4100 m, 01 Apr 1979, *Holm-Nielsen 16416* (AAU); Cordillera de los Llanganatis, NE side of Laguna Encantada, 01°11'S, 78°12'W, 3430 m, 16 Mar 1983, *Holm-Nielsen et al. 41858* (AAU); around Laguna Yuragcocha, 3 km E of the peak of Cerro Quilindaña, Cordillera Oriental, 00°47'S, 78°21'W, 4100 m, 31 Mar 1979, *Løjtnant & Molau 11567* (AAU); Volcán Antisana, rocky slopes on the W side of the mountain, 00°30'S, 78°10'W, 4500–4550 m, 21 Jul 1997, *Sklenar & Sklenarova 2803* (UC); Volcán Antisana, rocky slopes on the W side of the mountain, 00°30'S, 78°10'W, 4500–4550 m, 21 Jul 1997, *Sklenar & Sklenarova 2806* (UC).

Pichincha: heading down W-SW from the highest point of Sincholagua, 00°35'S, 78°21'W, 4600 m, 02 Jun 1985, *Bosco Nowak 171* (QCA); NE side of Cayambe mountain, 4420 m, 10 Dec 1961, *Cazalet & Pennington 5750* (B, UC); Volcán Atacazo, SW slope, Km 19 from San Juan, 00°21'S, 78°39'W, 2900 m, 25 Aug 1980, *Holm-Nielsen & Azanza 25180* (AAU); Nevado Cayambe, ladera S, 00°00.5'N, 78°00.95'W, 3700–3800 m, 29 Jun 2002, *Lehnert 108* (GOET, QCA, UC); "In Monte Pichincha," 3500 m, 1921, *Mille s.n.* (P). **Pichincha/Cotopaxi:** NE slope of Illiniza Sur, 00°40'S, 78°42'W, 4400 m, 28 May 1995, *Sklenar & Sklenarova 19_2* (UC). **Pichincha/Napo:** W side of a mountain ridge, ca. 2 km to the W from cerro Sara Urcu, 00°06'S, 77°57'W, 4400 m, 29 Aug 1995, *Sklenar & Kosteckovar 100-9* (AAU). **Tungurahua:** Volcán Tungurahua, N side of the mountain, steep slope to the right of the summit, 01°27'S, 78°27'W, 4100 m, 08 Aug 1997, *Sklenar & Sklenarova 3207* (UC).

Melpomene vulcanica Lehnert, *sp. nov.* TYPE.—ECUADOR. **Napo:** road Olmedo-Laguna San Marcos, E of the pass, 00°07'N, 77°59'W, 3640 m, 08–09 Jul 1980, *Ollgaard et al. 34159* (holotype: AAU; isotype: QCA). **Figs. 11, 12D.**

A *Melpomene pseudonutante* (Christ & Rosenst.) A. R. Sm. & R. C. Moran frondibus lanceolatis basin versus truncatis vel breve cuneatis (vs. frondibus longe obovatis basin versus decurrentibus) rhizomatibusque tenuioribus (0.8–1.5 mm vs. 1.8–2.5 mm), a *M. personata* pilis laminarum abaxialium aequaliter dispersis (vs. pilis in soris confertis) frondibusque erectis (vs. pendentibus) differt.

Plants epiphytic or terrestrial, in mosslayers on trunks of trees or the caudices of *Blechnum*, in ditches, sometimes directly rooting in soil. *Rhizomes* horizontal, moderately to long-creeping, regularly branching at wide to right angles, (0.8–)1.2–1.5 mm diam. (Fig. 11A, B). *Fronds* 10–25 cm long, erect, inserted onto the rhizomes at right angles, or at narrow angles and strongly ascending, diffusely placed (internodes (2–)10–20 mm) (Fig. 11A). *Scales* 3.5–6.2 × 0.6–1.0 mm, (18–)20–30(–46) cells wide, clathrate, cell walls thick and dark brown to thin and brown, weakly iridescent, broadly lanceolate to ovate-lanceolate, cordate to pseudopeltate at bases, acute to attenuate at the flat to flaring tips (Fig. 11C); apical cells 3–8 (rarely more), palmately or linearly arranged, relatively small and ephemeral. *Petioles* (20–)35–65(–80) mm long, 0.6–1.0 mm thick, marginate from the laminar bases to semiterete, glabrescent to hairy, with brown, acicular or ciliform hairs 1.0–1.5 mm long (Fig. 11D); simple and branched clavate hairs to 0.2 mm long rarely present; petiolar bases with scales. *Laminae* (45–)90–220 × (10–)16–30(–34) mm, lanceate (broadest below the middle, normally after the second segment pair), rather abruptly ending at bases, truncate or widely cuneate, acute to attenuate at tips (Fig. 11A). *Rachises* dark brown to black, planar and slightly sunken adaxially (Fig. 11E), hemispherically protruding abaxially (Fig. 11F), with scattered, brown, setiform/ciliform hairs 1.0–1.2 mm long. *Segments* (9.0–)10.0–14.5 (–17.0) × (2.8–)3.2–3.8 mm (ca. 3–4 times longer than broad), patent to ascending (80–60°), inequilateral, decurrent towards the bases, fully adnate, long-deltate to linear-oblong, the tips acute (Figs. 35E, F), in smaller fronds also obtuse; segments abaxially with scattered hairs like those on the rachises; midveins black, visible at least abaxially, in large fronds usually well visible from both sides with some scattered hairs like those on the rachis (Fig. 11F);

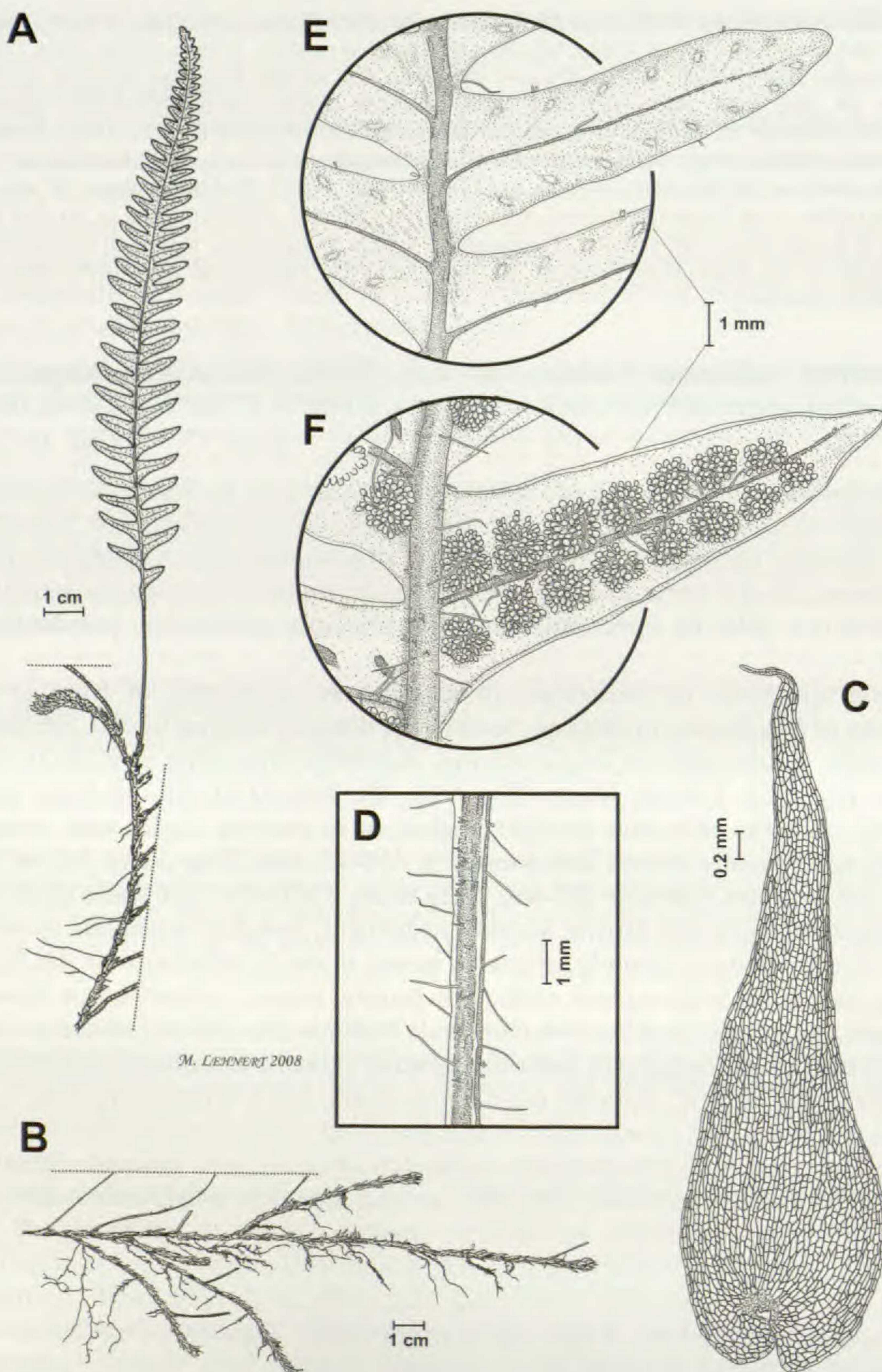


FIG. 11. *Melpomene vulcanica*. A. habit (Øllgaard et al. 34159, AAU); B. strongly branching rhizome, green fronds not shown (Lehnert 174, GOET); C. scale (Holm-Nielsen et al. 17235, AAU); D. petiole (Holm-Nielsen et al. 17235, AAU); E. segment adaxially (Holm-Nielsen et al. 17235, AAU); F. segment abaxially, sporangia immature (Øllgaard et al. 34159, AAU).

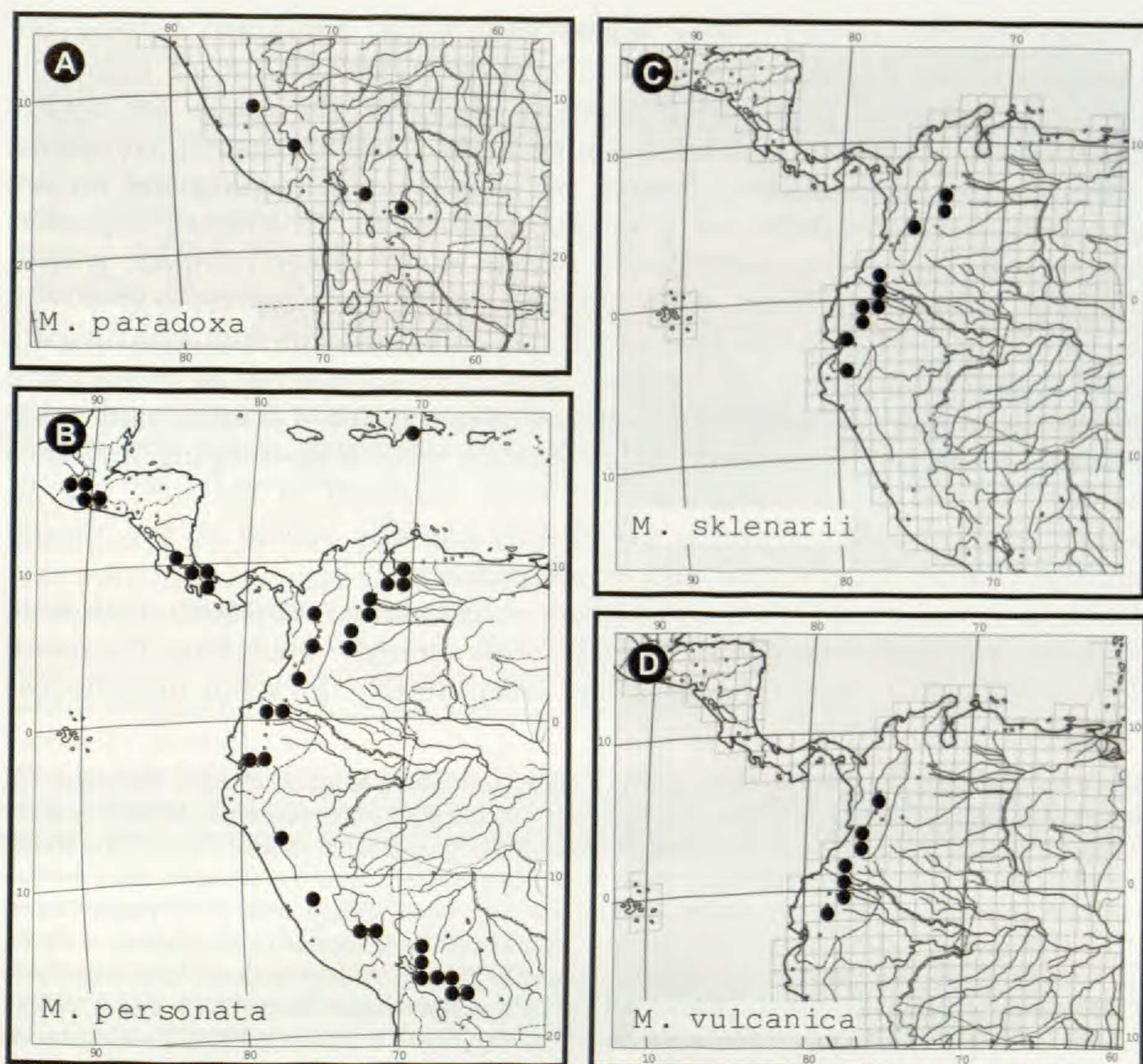


FIG. 12. Distribution of the new species. A. *Melpomene paradoxa*. B. *Melpomene personata*. C. *Melpomene sklenarii*. D. *Melpomene vulcanica*.

segment margins hyaline, (1–)2 cells wide, with few clavate hairs; proximal 1–3 pairs markedly smaller than the subsequent segments, but not auriculiform. *Sori* 2–4 pairs per segment, surrounded by (0–)2–8 brown setiform/ciliform hairs to 1.2 mm long (Fig. 11F).

The name refers to the fact that this species has been found mainly on the slopes of volcanoes.

Melpomene vulcanica grows in páramos and elfin forests at (2600–)3200–4500 m in Colombia and Ecuador (Fig. 12D).

The size of the laminae and the thickness of the cell walls in the scales vary considerably in this species, and every extreme of one character can be found within the whole range of the other without apparent correlation to the life form. However, plants with large fronds seem to grow in sheltered spots, i.e., they are present in nearly all epiphytes, but also in terrestrial plants from rock gullies. Smaller scales with thick cell walls are found in terrestrial plants

growing directly on soil; large scales with wide, iridescent lumina are produced if the rhizomes grow in thick moss layers, i.e., in all epiphytes and some terrestrial plants from páramos. However, the scales are always larger than in *M. sklenarii*, which is similar to the small forms of *M. vulcanica*.

Rhizomes of *Melpomene vulcanica* are usually long-creeping and do not bear any developed fronds over a length of the apices. This clearly separates this species from *M. pseudonutans*, which has a rather compact growth (although the posterior parts of the rhizome persist and contribute greatly to the total length). *Melpomene pseudonutans* also has thicker rhizomes (usually more than 2.0 mm diam. vs. usually less than 1.5 mm in *M. vulcanica*), thicker, less hairy petioles (1.0–1.2(–1.8) mm vs. 0.6–1.0 mm), and long-obovate blades (vs. lanceolate). Other species with long-creeping rhizomes similar to those of *M. vulcanica* have hairs clustered in the sori, like *M. personata*, and/or the midveins not or only partially visible on the abaxial laminae, like *M. flabelliformis* and *M. moniliformis*.

Øllgaard et al. 1194 (AAU) and *Sklenar & Sklenarova 3019* (UC), both from Ecuador, are good examples of plants with strongly branching rhizomes. *Bishop 1986* (UC), from Colombia, has exceptionally thick but nevertheless long-creeping rhizomes.

ADDITIONAL SPECIMENS EXAMINED.—COLOMBIA. **Cauca:** Cordillera Central, Parque Nacional del Puracé, camino de Pimabalá al volcán del Puracé, 3700 m, 19 Jul 1976, *Jaramillo Mejia & van der Hammen 5218* (COL); left side of road Tóez-Tacueyo, 3640 m, Sep 1980, *Rangel 2396* (COL). **Huila:** Cordillera Central, Cordillera del Buey, hike from Finca Loyola over the páramo down to San Antonio (2100 m according to residents), 2600 m, 14 Dec 1975, *Bishop 1986* (UC). **Huila-Cauca:** Macizo Colombiano, páramo Las Papas, cerros y alrededores de la laguna La Magdalena, 3530 m, 16 Oct 1958, *Idrobo et al. 2954* (AAU). **Nariño:** Páramo El Tabano, Alto de la Cordillera, entre Pasto y El Encano, vertiente occidental, 3200 m, 11 Jan 1941, *Cuatrecasas 11920* (COL); Pasto, Volcán Galeras, páramo al S de la cima, 3700 m, 24 Dec 1972, *Hagemann & Leist 1783* (COL); vertientes de Cumbal, 3400–4300 m, 22 Jan 1973, *Hagemann & Leist 1974* (COL). **Risaralda:** Santa Rosa, Cordillera Central, entre la hacienda La Sierra y Termales de Santa Rosa, Quebrada La Sierra, 3525 m, 26 Jan 1980, *Jaramillo Mejia et al. 5931* (COL).

ECUADOR. **Carchi:** Páramo El Angel, in the pass on road El Angel-Tulcán, 00°41'N, 77°54'W, 3750–3850 m, 15 May 1973, *Holm-Nielsen et al. 5476* (AAU); carretera Tufiño-Maldonado-Lagunas Verde, 01°28'S, 79°13'W, 3900–4000 m, 01 Oct 1994, *Navarrete 756* (AAU); Volcán Chiles, along gully on the SW side of the volcano, 00°48'N, 77°57'W, 4150–4200 m, 23 Jun 1995, *Sklenar & Sklenarova 637* (UC). **Chimborazo:** El Altar, N side of the volcano, on the ridge below the Canoningo peak, 01°41'S, 78°24'W, 4200–4400 m, 19 Aug 1995, *Sklenar & Kosteckovar 950, 93–15* (UC). **Imbabura:** E slopes of Cayambe peak, 3200 m, 16 Jul 1944, *Wiggins 10407* (NY). **Morona-Santiago:** trail Alao-Huamboya, around the pass, between Cuspipaccha and alt. 3700 m on E slope, 01°47'S, 78°25'W, 3550–3950 m, 07 May 1982, *Øllgaard et al. 38233* (AAU); trail Alao-Huamboya, around the pass, 01°47'S, 78°25'W, 3550–3950 m, 07 May 1982, *Øllgaard et al. 38290* (AAU); Cerros Yuibug-Pailacajas, E side of the mountain ridge, 01°45'S, 78°27'W, 4300 m, 31 Jul 1997, *Sklenar & Sklenarova 2968* (UC). **Napo:** Cordillera de los Llanganates, loma between Río Topo and Río Verde Grande, 3 km WNW of Cerro Hermoso, 01°13'S, 78°18'W, 4000 m, 10 Nov 1980, *Holm-Nielsen & Jaramillo J. 28329* (AAU); Cordillera de los Llanganatis, NE side of Laguna Encantada, 01°11'S, 78°12'W, 3430 m, 16 Mar 1983, *Holm-Nielsen et al. 41769, 41802, 41811, 41842* (AAU); S side of the crater of Cerro Sumaco, 00°34'S, 77°43'W, 3780–3820 m, 26 Apr 1979, *Holm-Nielsen et al. 17334* (AAU); E side of Cerro Sumaco, 00°34'S, 77°43'W, 3750 m, 30 Apr 1979, *Holm-Nielsen et al. 17469* (AAU); SE side of Cerro Sumaco, 00°34'S, 77°43'W, 3750 m, 30 Apr 1979, *Holm-Nielsen et al. 17489* (AAU); *ibid.*, 3750–3800 m, 01 May 1979, *Holm-Nielsen et al. 17550, 17577, 17590*

(AAU); *ibid.*, 3200 m, 02 May 1979, *Holm-Nielsen et al.* 17699 (AAU); *ibid.*, 3350 m, 05 May 1979, *Holm-Nielsen et al.* 17969 (AAU); carretera Quito-Baeza, Quijos, 4300 m, 08 Jul 2002, *Lehnert* 176 (GOET, QCA, UC); N-facing slopes at the W side of Laguna Paracocha, 00°16'S, 78°09'W, 4100 m, 18 Mar 1979, *Løjtnant & Molau* 11164 (AAU); NE-facing ridge on the N side of Cerro Sumaco, 00°35'S, 77°39'W, 3600–3700 m, 24 Apr 1979, *Løjtnant & Molau* 12664 (AAU); S side of Cerro Sumaco, 100–200 m S of the main crater, 00°35'S, 77°39'W, 3700–3800 m, 29 Apr 1979, *Løjtnant & Molau* 12954B, 12954C (AAU); Oyacachi, 5 km después del paso, bosques en los márgenes del carretero, 00°12'S, 78°06'W, 3500 m, 28 Dec 1996, *Navarrete* 1367 (AAU, QCA); Oyacachi, Yarupaccha, 00°12'S, 78°07'W, 3620–3680 m, 16 Jan 1996, *Navarrete* 1416 (AAU), road Quito-Baeza, 7–8 km NW of the Laguna Papallacta (Páramo de Guamani), 00°19'S, 78°08'W, 3800 m, 20 Jul 1976, *Øllgaard & Balslev* 8162 (AAU); Páramo de Soguillas, near Las Torres de Llanganati, 01°08–09'S, 78°15–16'W, 3850–4000 m, 16–17 May 1982, *Øllgaard & Holm-Nielsen* 38752 (AAU); Llanganati, páramo SE of Chosa Aucacocha, between Aucacocha and Pan de Azúcar, 01°09'S, 78°18'W, 3800–3900 m, 15 May 1982, *Øllgaard et al.* 38496 (AAU); Volcán Antisana, rocky gully on the W side of the mountain, 00°30'S, 78°10'W, 4400–4500 m, 22 Jul 1997, *Sklenar & Sklenarova* 2784 (AAU, UC); NE side of Volcán Antisana, 00°27'S, 78°08'W, 4300 m, 17 Aug 1997, *Sklenar & Sklenarova* 3402 (AAU, UC); *ibid.*, 00°27'S, 78°08'W, 4200 m, 18 Aug 1997, *Sklenar & Sklenarova* 3438 (AAU, UC); Hacienda Yanahurco, 3800 m, 28 Aug 2001, *Smith A. R. et al.* 2875 (UC). **Pichincha:** Guamani pass, E of Pifo, Cordillera Oriental, 4000 m, 10 Nov 1944, *Ewan* 16447 (UC); 2 km S of Paso de la Virgen on road Quito-Baeza, 00°20'S, 78°13'W, 4000–4200 m, 19–20 May 1984, *Laegaard* 52148 (AAU); Carretera Quito-Baeza, 00°20.2'S, 78°13.2'W, 4200 m, 08 Jul 2002, *Lehnert* 168 (GOET, QCA, UC); *ibid.*, Km 256, 4300 m, 08 Jul 2002, *Lehnert* 174 (GOET, QCA, UC); Páramo de Guamaní, Carretera Pifo-Papallacta, 00°19'S, 78°12'W, 3960 m, 13 Jan 1990–26 May 1991, *León S.* 1164 (AAU); Volcán Cayambe, N slopes, 00°03–05'N, 77°59'W, 3750–3850 m, 09 Jul 1980, *Øllgaard et al.* 34235A (AAU); road and trail from Chaupi-páramo of Volcán Corazón, 00°34'S, 78°41'W, 4140 m, 15 Mar 1995, *Øllgaard et al.* 1194 (AAU); W side of a mountain ridge ca. 2 km to the west from Cerro Sara Urcu, 00°06'S, 77°57'W, 4100 m, 30 Aug 1995, *Sklenar & Sklenarova* 108–2 (AAU); Pichincha/Napo border, edge of Antisana reserve, 3800 m, 28 Aug 2001, *Smith A. R. et al.* 2871 (UC); along road Quito-Pallapacta, 2800–3900 m, 27 Feb 1994, *van der Werff & Gray* 13356 (UC); at pass of road Quito-Pallapacta, 4000 m, 14 Jul 1991, *van der Werff & Palacios* 12357 (AAU). **Pichincha/Napo:** Volcán Cayambe, N slopes, 00°03–05'N, 77°59'W, 3750–3850 m, 09 Jul 1980, *Øllgaard et al.* 34290 (AAU); road Olmedo-Laguna San Marcos, E of the pass, 00°07'N, 77°59'W, 3620–3800 m, 10–11 Jul 1980, *Øllgaard et al.* 34462 (AAU); W side of a mountain ridge, ca. 2 km to the west from cerro Sara Urcu, 00°06'S, 77°57'W, 4400 m, 29 Aug 1995, *Sklenar & Kosteckovar* 1118 (AAU). **Tungurahua:** Santiago de Pillaro Cantón, páramos de Pisayambo, surroundings of laguna de Pisayambo, 01°05'S, 78°23'W, 3600–3900 m, 11 Oct 1998, *Cueva* 249 (UC); Santiago de Pillaro, Parque Nacional Llanganates, W of Cerro Hermoso, near saddle between headwaters of Río Verde and Río Topo, 01°11'40"S, 78°19'34"W, 3950 m, 12 Nov 1999, *Neill et al.* 12005 (UC); Cerro Hermoso, SW ridge of the mountain, 01°14'S, 78°18'W, 4100 m, 06 Sep 1997, *Sklenar & Sklenarova* 3625 (AAU); Patate Cantón, Parque Nacional Llanganates, slopes of Cerro Pan de Azúcar, on transect Páramo de Soguillas-Cerro Pan de Azúcar, 01°09'S, 78°17'W, 3800 m, 13 Oct 1998, *Vargas H. et al.* 2820 (UC).

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